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THE UNIVERSITY OF ALBERTA

THE GENERA OF THE HOLARCTIC ELAPHRINI AND SPECIES OF ELAPHRUS FABRICIUS (COLEOPTERA:CARABIDAE): CLASSIFICATION, PHYLOGENY, AND ZOOGEOGRAPHY

by

© HENRI GOULET

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA
SPRING, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Genera of the Holarctic Elaphrini and Species of Elaphrus Fabricius (Coleoptera: Carabidae): Classification, Phylogeny, and Zoogeography submitted by Henri Goulet in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

The tribe, genera, and subgenera are redefined based on characteristics of adults and larvae. Four subgenera of Elaphrus Fabricius 1775 are recognized: Arctelaphrus Semenov 1926, Neoelaphrus Hatch 1931 with three species groups, Elaphrus, and Elaphroterus Semenov, 1895. Recognized are 34 species and 2 subspecies. Keys are given to elaphrine genera, and to subgenera, species and subspecies of Elaphrus for adults and known larvae.

Described as new is E. lindrothi (type locality: United States: Maryland, Bowie). Synonymies proposed for the first time are: subgenus Elaphrotatus Semenov 1895 = Elaphroterus Semenov. Elaphrus ruscarius foveatus Pierce 1948 = Elaphrus finitimus Casey 1920; Elaphrus clairvillei lynni Pierce 1948 = Elaphrus clairvillei Kirby 1837.

Given for each species as appropriate are: synonymic list, diagnostic combination and description of adults and larvae, discussion of variation, derivation of the specific epithet, geographic distribution, collecting notes, and taxonomic notes. Important structural characteristics are illustrated. Geographic distributions are mapped for all North American species of Arctelaphrus and Neoelaphrus. Descriptions of most species are augmented with tables of descriptive statistics. Results of detailed statistical analyses of geographic variation are mapped and discussed for members of some North American species.

Relationships of genera and subgenera of Elaphrini are established using separately the procedures of phenetic and evolutionary-cladistic systematics based independently on characteristics of adults and larvae. The phenetic systems of association based on adults and larvae are incongruent at the generic level but congruent at the subgeneric level. The cladistic systems of association based on adults and larvae are congruent, and differ from the phenetic system at the generic level and in associating *Neoelaphrus* at the subgeneric level. The incongruent phenetic systems are explained in terms of evolutionary rates. A phylogeny is reconstructed for genera, subgenera and species of *Arctelaphrus* and *Neoelaphrus* based on structural characteristics of adults and larvae. From the reconstructed phylogeny an arrangement is established for the three genera and four subgenera of *Elaphrus*.

It is hypothesized that the ancestral elaphroid stock (the elaphrine ancestor and its sister group) evolved and radiated in tropical Asia where it became extinct except for the immediate ancestor of the elaphrines surviving in temperate northernmost central Siberia in the Late Cretaceous. There it radiated and gave rise to extant genera and subgenera. In the Oligocene, as the temperate zone was expanding, the ancestor of *Neoelaphrus* reached Beringia and by the Early Miocene separated into two lineages. The Asiatic lineage gave rise to extant members of the *uliginosus* group while the North American lineage gave rise to two lineages: the fuliginosus group associated with the mixed mesophytic forest, and a more cold hardy lineage, the cupreus group. The cupreus stock extended over cold temperate Beringia in the Late Miocene. The stock was divided by continued climate deterioration giving rise to the sibiricus lineage in Asia and the clairvillei lineage in North America. The history of elaphrine evolution is a succession whereby ancestral peripheral elements extend into areas of low competition pressure followed by radiation. This pattern was repeated with the formation of the cold temperate, Boreal and arctic zones. The pattern is basically in one direction from areas of intense competition to areas of less competition (smaller land masses, new climatic zones, high altitude regions, or peat bogs).

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1.0 Introduction

Since capturing my first Elaphrus Fabricius 1775 specimen in 1962, I have remained excited by these little jewels. Adults of most species are beautifully sculptured, and some brilliantly coloured. Moreover, the marked specialization in habitat requirements of many species fascinated me (Goulet, 1964).

Adults of Elaphrus are extremely easy to recognize because of their cicindeloid shape, and because of the four rows of very large elytral depressions (pits). However, North American species of the subgenus Elaphrus could not be identified until Lindroth's (1961a) superb review. Pronotal shape, a character used extensively by earlier authors, along with inadequate descriptions, and very few specimens, contributed to confusion among taxonomists. Many names were created during the 1800's, of which about 45% apply to recognized taxa. In the early 1900's, the confusion became worse as only 15% of the then described taxa are recognized today. The taxonomic situation discouraged entomologists from studying these beetles except for a few rather distinct taxa described in the past 30 years. Lindroth, in his revision, recognized 14 North American taxa and suggested problems in need of taxonomic study. He laid solidly the ground for further studies. In part, if I was able to see more, it was because I was standing on the shoulders of this giant.

This work is intended as a continuation of Lindroth's work. I deal more with intraspecific variation, larvae, behavior, and habitat requirements. Although I focus much of my efforts on North American species, I include all Euroasiatic taxa known to me. However, I have not included detailed treatment of the species of *Elaphrus* (*sensu stricto*) or *Elaphroterus*. I made a special effort to gather large amounts of structural evidence on adults and larvae, not only to test independently phylogenetic reconstructions for congruency but also to help students of fossil insects, who must work with fragments of specimens. These data should help place Lindroth's classification of genera and subgenera of the world Elaphrini on a more solid base. I discuss phyletic relationships between species of each subgenus and attempt to trace past zoogeographical events.

Cicindela riparia Linnaeus, 1758, was the first formally recognized species of *Elaphrus*. Fabricius (1775) erected the genus *Elaphrus* to include the above species and others that are today in *Notiophilus* Duméril, 1806, and *Bembidion* Latreille, 1802; and described *E. uliginosus* Fabricius. Latreille (1810) established *E. riparius* as type species, and excluded *Bembidion* from *Elaphrus*. Dejean (1826) published the first revision and restricted *Elaphrus* to its present concept. Some authors after Dejean used the genus *Elaphrus* in a wider sense: Brullé (1834) included *Pelophila* Dejean, 1828, and *Blethisa* Bonelli, 1810; and Lacordaire (1854) added *Opisthius* Kirby, 1837. However, Dejean's concept was generally accepted.

It became apparent to Semenov (1895, 1926), who was studying the very rich Russian Elaphrus fauna, that there were natural groups among the species, and he arranged the species in five subgenera. Hatch (1951) published two nomenclature changes. Larvae were first described by Schiödte (1867). Major advances in knowledge of larvae were made by Van Emdem (1942), Lindroth (1954), and Luff (1976), and now all elaphrine genera and subgenera can be recognized.

From the mid 1800's, numerous local faunas mostly in Europe were published (Csiki, 1933, mentioned all older faunas; Antoine, 1955; Chagnon and Robert, 1962, Freude et al., 1976; Hatch, 1953; Jeannel, 1941, 1942; Lindroth 1961, 1974; and Nakane, 1973). In a few recent works, the precise habitat is described, but Lindroth (1949), Goulet (1964), and especially Bauer (1974) provided much insight about behaviour, ecological relationships, and dispersal potential of some species of Elaphrus.

In this study, I provide the basis for a similar study of the Asiatic fauna. I hope that my work will not only make possible identification of specimens, but also stimulate more detailed investigations into the many problems in evolutionary biology that render members of this genus so interesting. Thus, I have attempted to unravel some of the many puzzles in speciation of North American Elaphrus, to put on a firmer base the Euroasiatic Elaphrus complex, and to point out the many problems that demand particular attention.

2.0 Materials and Methods

2.1 Materials

I based this study on about 18,000 adults (1500 European) and 400 larvae (20 European). Most specimens of adult beetles were loaned to me by various institutions and private collections in Canada, United States, and Europe. Others came through collecting by G. E. Ball, J. Belicek, H. E. Frania, F. Goulet, D. H. Kavanaugh, and myself. Larval material came mostly from my collection (most of them _ex ovo_) and very important material from C. H. Lindroth (Sweden) and T. Bauer (Austria). Fossil fragments from Pleistocene and Pliocene deposits were provided by J. V. Matthews, A. Morgan, A. Ashworth, and R. E. Morlan. The following abbreviations, mostly from Arnett and Samuelson (1961), represent these collections and their respective curators.

ALar College Bourget, C.P. 1000, Rigaud, Quebec;

AMNH Department of Entomology Collection, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024; L. H. Herman.

ANSP Department of Entomology Collection, Academy of Natural Sciences, 19th and Parkway, Philadelphia, Pennsylvania 19103; M. G.. Emsley.

BMCS Musee d'Histoire Naturelle de Bale, Bale Suisse; W. Whittmer.

BMNH	Department of Entomology, British Museum of Natural History, Cromwell Road, London, SW.7 5BD, England; R. Aldridge.
BMSC	Buffalo Museum of Science, Humbolt Park, Buffalo, New York 14211; H. W. Charnley.
BMUW	Burke Museum, Department of Zoology, University of Washington, Seattle, Washington 98105; M. H. Hatch.
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; D. H. Kavanaugh.
CDAE	Bureau of Entomology, State of California, Department of Agriculture, 1220 N. St., Sacramento, California 95814; T.N. Seeno.
CISC	California Insect Survey, Division of Entomology and Acarology, University of California, Berkeley, California 94720; J. A. Chemsak.
CNCI	Canadian National Collection of Insects, Biosystematics Research Institute, Canada Department of Agriculture, Ottawa, Ontario K1A 0C6; J. E. H. Martin.
CSLB	Entomological Collections, California State College at Long Beach, Long Beach, California 90801; E. L. Sleeper.
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14850; L. L. Pechuman.
DEFW	Department of Entomology, Fisheries and Wildlife Collection, University of Minnesota, St. Paul,

	Minnesota 55101; P. J. Clausen.
DEUN	Department of Entomology Collection, University of Nebraska, Lincoln, Nebraska 68503; B. C. Ratcliffe.
DHKa	D. H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118.
DMNH	Dayton Museum of Natural History, 2629 Ridge Ave., Dayton, Ohio 45414; E. J. Koestner.
DRWh	D. R. Whitehead, Division of Forest Identification, Agricultures Research Service, c/o United States National Museum, Washington, District of Columbia 20560.
DZEC	Department of Zoology and Entomology Collection, Montana State University, Bozeman, Montana 59715; N. L. Anderson.
EJKC	E. J. Kitely, 16-13th Street, Roxboro 900, Quebec.
EMUS	Entomology Museum, Department of Zoology, Utah State University, Logan, Utah 84321; W. J. Hanson.
ESUW	Entomology Section Museum, Plant Sciences Division, University of Wyoming, Laramie, Wyoming 83070; R. J. Lavigne.
FGAC	F. G. Andrews, Department of Food and Agriculture, 1220 N. Street, Sacramento, California 95814.
FMNH	Insect Collection, Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605; H. S. Dybas.
FNYC	F. N. Young, Department of Zoology, Indiana University,

	Bloomington, Indiana 47401.
FRLC	Forest Research Laboratory Collection, Box 4000, Fredericton, New Brunswick; G. R. Underwood.
HGou	H. Goulet, Department of Entomology, University of Alberta, Edmonton, Alberta.
HHCC	H. Hacker, 235 Randall St., San Francisco, California 94 131.
ICCM	Section of Insects and Spiders, Carnegie Museum, Pittsburg, Pennsylvania 15213; G. E. Wallace.
INHS	Insect Collection, Illinois State Natural History Survey, Urbana, Illinois 61803; M. W. Sanderson.
ISUI	Department of Zoology and Entomology Collection, Iowa State University, Ames, Iowa 50010; J. L. Laffoon.
JBel	J. Belicek, Department of Entomology, University of Alberta, Edmonton, Alberta.
JMCi	J. M. Cicero, 13641 Terrace Bella St., Pacoima, California 91331.
JSCC	Joe Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.
JVMa	J. V. Matthews, Jr., Geological Survey of Canada, 601 Booth Street, Ottawa, Ontario.
KSUC	Department of Entomology Collection, Kansas State University, Manhattan, Kansas 66502; H. D. Blocker.
LACM	Insect Collection, Los Angeles County Museum of Natural Hisotry, 900 Exposition Blvd., Los Angeles, California 90007; C. L. Houes.
LSUC	Department of Entomology Collection, Louisiana State

	University. Baton Rouge, Louisiana 70803; B. T. Chapin.
MCPM	Milwaukee City Public Museum, 800 West Wells St., Milwaukee, Wisconsin 53233; K. W. MacArthur, G. R. Nooron.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachussets 02138; J. L. Lawrence.
MSUC	Department of Entomology Collection, Michigan State University, East Lansing, Michigan 48823; E. R. Hoebeke.
NCSU	Department of Entomology Collection, North Carolina State University, Raleigh, North Carolina 27607; D. A. Young.
NDSU	Entomology Department Collection, North Dakota State University, Fargo, North Dakota 58102; R. L. Post.
NMDC	N. M. Downie, 505 Lingle Terrace, Lafayette, Indiana 47901.
NSMC	Insect Collection, Nova Scotia Museum, Halifax, Nova Scotia; L. Martin.
OSEC	Department of Entomology Collection, Oklahoma State University, Stillwater, Oklahoma 74074; W. A. Drew.
OSUC	Ohio State University Collection of Insects and Spiders, 1735 Neil Ave., Columbus, Ohio 43210; A. A. Triplehorn.
PADA	Insect Collection, Bureau of Plant Industry, Pennsylvania Department of Agriculture, 2301 North Cameron St., Harrisburg, Pennsylvania 17120; T. J. Henry.

PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; K. W. Brown.
PSUC	Department of Entomology Collection, Pennsylvania State University, University Park, Pennsylvania 16802; K. C. Kim.
PURC	Entomology Research Collection, Department of Entomology, Purdue University, Lafayette, Indiana 47907; A. Provonsha.
RFCC	R. Freitag, Department of Biology, Lakehead University, Thunder Bay, Ontario.
ROMC	Royal Ontario Museum, University of Toronto, Toronto 5, Ontario; G. B. Wiggins.
SEMC	Snow Entomology Museum, Univeristy of Kansas, Lawrence, Kansas 66044; P. D. Ashlock.
SFAC	Department of Biology Collection, Stephen F. Austin State College, Nacogdoches, Texas 75961; W. W. Gibson.
TBau	T. Bauer, I. Zoologisches Institut der Univeritat Wien, Wien, Austria.
UADE	Department of Entomology Collection, University of Arkansas, Fayetteville, Arkansas 72701; E. P. Rouse.
UASM	Department of Entomology, University of Alberta, Strickland Museum, Edmonton, Alberta; G. E. Ball.
UBCZ	Spencer Entomology Museum, Department of Zoology, University of British Columbia, Vancouver 8, British Columbia; G. G. E. Scudder.
UCDC	Department of Entomology Collection, University of California, Davis, California 95616; R. O. Schuster.

UCEC Department of Entomology Collection, University of Colorado, Boulder, Colorado 80302; U. N. Lanham.

UCRC Department of Entomology Collection, University of California, Riverside, California 92502; S. I. Frommer.

UICM Department of Entomology Collection, University of Idaho, Moscow, Idaho 83843; W. F. Barr.

ULIC Department of Biology Insect Collection, University of Louisville, Louisville, Kentucky 40208; C. V. Covell.

UMMZ Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104; R. S. Alexander.

UMRM Entomology Research Museum, 1-87 Agriculture Building, University of Missouri, Columbia, Missouri 65201; W. R. Enns.

USNM Division of Coleoptera, Department of Entomology, United States National Museum, Washington, District of Columbia 20560; P. J. Spangler.

UVCC Department of Zoology Collection, University of Vermont, Burlington, Vermont 05401; R. T. Bell.

UWOC Department of Zoology Collection, University of Western Ontario, London, Ontario; W. W. Judd.

UWEM Entomology Museum, Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706; W. J. Bayer.

UMKC V. M. Kirk, Northern Grain Insect Research Laboratory, Brookings, South Dakota 57006.

UZMF Universitetets Zoologiska Museum, Entomologiska Avdelningen, N. Jarnvagsgatan 13, SF-00100 Helsingfors 10, Finland; H. Silfverberg.

WSUC Department of Entomology Collection, Washington State University, Pullman, Washington 99163; M. T. James.

ZMLS Zoological Institute, Department of Systematics, University of Lund, Lund, Sweden; C. H. Lindroth.

2.2 Methods

2.2.1 Collection, Preservation and Mounting of Specimens

Collection.- Adults of all species live along rivers, small streams, in swamps, sloughs, and bogs, and on muddy surfaces. Where substrate is a thick organic layer, beetles were extracted by treading the vegetation under water. On substrates of very fine texture (clay, fine muds), treading is done slowly and gently moving in one direction to force the beetles out of cracks before being trod upon and buried. I used this technique only in sunny weather, because in cloudy or rainy conditions most beetles of these habitats are inactive.

In moist but not soggy bogs, pitfall traps were most productive because the vegetation could not be trod under water. I used pitfall traps with success in all habitats where Elaphrus populations live. In saturated or very wet habitats I used a special modification of pitfall trap requiring no digging (not described in this text)--such traps were effective even on water. To avoid bias in favor of the more active males or rarer color forms I attempted to collect all the beetles in the area.

Larvae live in the same habitats as adults, but different procedures were used to collect them. Some larvae enter pitfall traps, but a more fruitful method was to gently press by hand the organic beach many times at the same spot. This yielded numerous larvae especially those of the first instar. On fine textured soil or inorganic habitats, repeated splashings with water yielded larvae. I failed, or had very little success, with _Elaphrus purpurans_ Hausen, since the habitat of these insects is well drained upper beach; nor was I able to collect larvae of _E. lecontei_ Crotch. Most larvae were obtained through rearing. Females of the subgenera _Elaphrus_ and _Elaphroterus_ Semenov, 1895 oviposit, in captivity, on very moist absorbent paper after feeding; those of other elaphrines oviposit on moist soil especially if just freshly dampened (Goulet, 1976). These two techniques provide eggs of exact known age since oviposition is easily observed a few minutes after the fed beetles are put on the substrate.

Preservation and preparation.- Collected adults were killed in ethyl acetate and mounted uniformly on points after cleaning and dissecting the genitalia from some males. A few specimens were kept in 70% EtOH as vouchers for reared larvae or for dissection. Larvae were stored in 70% EtOH after they were left in boiling or very hot water for about five minutes. This insures that autolytic enzymes are destroyed, and, more importantly, that the body of a larva is straight. This technique is successful only with freshly killed larvae or those thrown in boiling water alive. A few larvae were dehydrated by freeze-drying or by chemical means, for study with the Scanning Electron Microscope (SEM) or for dry mounting with the specimens with the adult collection. Dr. T. Palm (Lindroth _in litt_.) suggested the following simple method:

1. Transfer larvae step by step (about 24 hours/step) through the following agents: a) alcohol 80%, b) absolute alcohol, c) mixture of absolute alcohol and xylene, and d) pure xylene.
2. Dry specimen on filter paper and glue to a piece of cardboard (as for mounting adults in Europe).

For detailed studies of larvae, I mounted them in glycerin. With this method body proportions are preserved and the same specimen can be studied and moved easily to different angles.

Larvae. To insure satisfactory results clean all containers and pipettes.

1. If a larva is 5 to 10 mm long, pierce the body ventrally or laterally in the thorax. If larger (10 to 20 mm) pierce and enlarge opening in the abdomen. This facilitates the next step.
2. Place the larvae in gently boiling 10% KOH for 3 to 5 minutes.
3. Transfer larvae into distilled water with a wide mouthed eye-dropper thus avoiding collapse of the body.

Neutralize KOH with acetic acid and/or change most of the water several times.

4. Transfer larvae with wide mouthed eye-dropper into 4% glycerin-water solution (V/V). The best receptacles are concave at the bottom.

5. Place the receptacle on a microscope slide drying plate where water will evaporate (60 C). Add more of the glycerin solution after a few hours. Twelve hours or less is enough to complete the glycerin concentration and impregnation process. The larvae are then ready to be transferred to a ringed slide for study.

The larvae can be preserved in closed vials of glycerin for at least two years. If larvae are to be stored indefinitely, they can be transferred to 70% alcohol, but for future studies, they must be reimpregnated by starting at step 4. If larvae are studied at magnifications below 400X, it is not necessary to use cover slips if glycerin is level with the upper edge of the ring. This greatly facilitates positioning of specimens. The ring should be made of a material that is chemically stable, or the larvae should be on the slide for less than a month.

2.2.1.1 Rearing of Larvae

The techniques for rearing elaphrines as well as other carabids have been described (Goulet, 1976). Larvae of most

North American *Elaphrus* were reared from eggs (except *E. lapponicus* Gyllenhal, *E. lindrothi* new species, *E.* species A, *E.* species B, *E. viridis* Horn and *E. parviceps* Van Dyke). The larvae of *E. lapponicus* were recognized by association (Lindroth, 1954). In addition, I studied the larvae reared from eggs of four Euroasiatic species (*E. cupreus* Duftschmid, *E. riparius* Linnaeus, *E. aureus* Mullër and *E. ulrichi* Redtenbacher). I reared from eggs *Diacheila polita* Faldermann, *Blethisa multipunctata* Linnaeus and *B. quadricollis Haldeman*, I also studied specimens of *B. julii* LeConte and the description of *Diacheila arctica* Gyllenhal recognized by association (Lindroth, 1954). The number of specimens for each larval instar and the locality of origin of these specimens or of the parents is given under "Distribution" for each taxon. The larvae reared for this study are obtained from a group of about ten females for each species.

2.2.2 External Structures of Adults and Larvae

I illustrate and briefly define structures that are unusual or rarely mentioned in faunal works. Basic external structures of adults are described by Lindroth (1969), and those of larvae by Van Emden (1942).

Sculpture of an elytron of a specimen of *Elaphrus* consists of four rows of circles (pits) and one to four rows of very strongly reflecting surfaces (mirrors)(Fig. 111 and

113). Pits of specimens of most species are distinctly outlined. At the middle of each pit (except the two humeral pits) is a setigerous puncture (Fig. 123). Lateral edges in specimens of some species are delimited by curved ridges. Mirrors are of similar width in specimens of some species while in others one or two mirrors are wider (Fig. 113 and 117). Mirrors are distinctly outlined if the punctures around them are sharply separated from the mirror surface; if the punctures are progressively more scattered toward the middle of the mirror, the mirror is indistinctly outlined. Mirrors are contrasted if the color of the mirror is clearly different from nearby surface color. In this study I retraced the origin of striae and intervals. Thus the rows of elytral pits and intervening areas are coded in function of the original system. The rows of pits and mirrors are in intervals 3, 5, 7 and 9, while the intervening areas are in intervals 1, 2, 4, 6 and 8.

The surface of the pronotum of most specimens of _Elaphrus_ shows, on the disc on each side of the middle, one to five extra depressions termed discal impressions (Fig. 17a and 105); in most specimens one sees a large impression near the middle of the disc on each side, and one small medial impression near the medial linear impression.

Setae are of two types: basic and accessory. Basic setae are those of most adult carabids, and first instar larvae. Accessory setae are those not or rarely found on adult carabids, or in larvae they are the setae additional to the basic setae in the second and third instars. In descriptions of larvae, accessory setae are either major or minor. Minor accessory setae are smaller than major ones and also are less consistent in number and position than major accessory setae. On larvae small circular hole-like structures the size of a setigerous puncture are termed pores. Basic pores found in first instar larvae are asetose, while accessory pores, have an extremely thin and small seta. (If in doubt I used the expression "absent or seta virtually absent"). Only basic setae and pores of larvae are coded.

Except for setae on the legs, nomenclature of setae on adults is well understood. Individual setae are not mentioned so the nomenclature applies to groups of setae i.e. rows, and fringes. Setae on coxae, trochanters and tarsi are easily located, but those of femora and tibiae are often very difficult to recognize. The position of a row is a function of the position of the femur or of the tibia. If legs of beetles are arranged vertically, the narrow edge of the femur facing upward is the external surface, the opposite surface is the internal one, the wide surface facing anteriorly is the anterior one, and the opposite surface is the posterior one. The same applies to the surfaces of tibiae and tarsomeres. Coded setal rows are illustrated in Fig. 145, 146, 147, and 148.

Nomenclature of setae and pores in larvae is a preliminary effort. I use similar designations for apparently homologous setae and pores. This system is based on the setae and pores of first instar larvae. Setae added in the second and third instars vary in position and number, to a lesser or greater extent. This basic larval system of setae and pores seems to be a common feature of larvae of Carabidae. I did not follow Habu's (1961) system for head setae, as it was incomplete.

Designation of setae and pores is derived from position. It begins with a coded name for the sclerite, followed by position of a small group of proximate setae and pores, and finally the position of the seta or pore inside the group i.e. Ab6T PII-P refers to a seta on abdominal tergum 6 on posterior row internally and is the posterior one in the group. I failed to homologize with other abdominal segments setae and pores on abdominal terga 9 and 10, and on sternum 10. Setae and pore codes are illustrated in Fig. 76.

Microsculpture of adults and larvae is highly varied. The terms used are briefly explained. Lines (or microscropic grooves) on many surfaces form hexagonal patterns. The outlines of these figures are termed meshes. Meshes are approximately circular (termed isodiametric) or stretched (termed transverse) (Fig. 151). The area inside the meshes is the alveola; its surface is flat, subconvex, or convex. Alveolae, if eccentrically convex and elevated on one side, achieve the appearance of the skin of a fish - termed scaly. The elevated edge of the scale-like alveolae may have one or more small to large points. In most cases, when the elevated edge is shaped like a point or points, the outlines of the alveolae are missing; thus I term this microsculpture single-pointed or multi-pointed (Fig. 152, 153, 154, 155, and 156).

Punctures are important surface features of adults of Elaphrus. Punctures are circular or elongate in outline. Their size is expressed as the diameter of the longest axis in microns (average values given in text). Their density is expressed as distance, in microns, between two punctures (in the text I give average values). Puncture edges are sharply outlined or, if rounded, indistinctly outlined; a sharp edge around half the circumference is termed: edge sharply outlined on 50% of circumference.

Some features of male genitalia were studied. I examined only the intromittent organ (the median lobe) and its closely associated parameres (Fig. 40). The spatula-like apex (in side view) is termed spatula or apex of median lobe. The internal sac is the soft membranous surface (adorned with setae, scales, sclerites, etc.) inside the median lobe; it is particularly eversible near apex of lobe. Most features of the internal sac could not be studied except for the enormous strut (termed stylet) extended through the base (basal orifice) of the median lobe (Fig. 39). In the text, the number of male genitalia studied referred to those studied completely (median lobe and parameres). However, I have seen many apices of median lobe (for any common species I saw 30 or more).

I follow Noonan's (1973) terms for the ovipositor except for the thickly sclerotized last two sclerites that form the stylus (Fig. 71). The anterior sclerite is termed basal sclerite, the posterior sclerite is termed apical sclerite. These two sclerites were referred to in generic and subgeneric descriptions. I failed to find useful characteristics in the internal genitalia. Few ovipositors were studied as I failed to see structural differences below subgenus level. I studied 1 to 3 ovipositors for most members of Elaphrini.

2.2.3 Measurements

2.2.3.1 Meristic, Mensural, and Class Characters

These data were obtained for adults with a Leitz stereoscopic microscope at magnifications of 12.5, 18, 50, 72, 150, and 216 diameters using a micrometer eyepiece with a scale interval of 0.05 mm at 18 diameters.

The following abbreviations indicate the measurements made for at least one sample of each Elaphrus species:

EL--Elytral length from apex of scutellum to apex of elytron.

EW--Elytral maximum width.

PL--Pronotal length from basal margin to anterior margin along the central furrow.

PW--Pronotal maximum width.

HW--Head maximum width between the external margins of the eyes.

These measurements were used unmodified, or in ratio combinations for statistical analysis, as follows: PL/PW, PL/EL, PL/EW, PL/HW, PW/EL, PW/EW, PW/HW, EL/EW, EL/HW, EW/HW.

The following measurements were recorded on the median lobes of male genitalia of some species:

ML--Median lobe length from the internal angle at base to apex of the lobe.

AL--Length of apical spatula from junction of the line of maximum width of this spatula.

AW--Maximum width of the spatula.

These measurements were also used unmodified, or in ratio combination for statistical analysis: EL/ML, EL/AL, EL/AW, ML/AL, ML/AW, AL/AW.

I recorded measurements on head capsules of first instar larvae. These measurements are illustrated in Fig. 77.

Measured characters were analyzed statistically. Meristic and class characters were expressed only as means, because the variance is much too high for interpretation (Mayr, 1969). Interpretation of these means as a measure of tendency is a function of variability inside samples, and degree of difference between samples. Thus, markedly different means within samples decrease the significance of the value observed between samples.

Measured data and their statistics enhance species descriptions, aiding in detection of potential gene flow. isolation between allopatric groups of specimens.

2.2.3.2 Descriptive Statistics

Except for one North American and one Euroasiatic species known from two specimens only, I present descriptive statistics of at least one sample of each species. For samples of eight specimens (total of males and females, or eight males, or eight females), I provide the following statistics of dispersion: range of variation, mean, two standard errors of the mean, 1.5 standard deviation, and coefficient of variation (Hubbs and Hubbs, 1953). Briefly, four standard errors of the mean difference between two means signify that the probability of these means being the same is only 5%, or insignificant. If two populations differ in a character measured by 3.0 standard deviations (assuming normal distribution), then 90% or more of the specimens in one sample are likely to be different from 90% or more of the specimens in the other population.

I followed Whitehead (1971) in determining sample size and its assembly. Ideally, 10 males and 10 females collected in one locality at one time were used. If necessary, specimens from localities in geographically homogeneous areas were assembled to make a sample. Finally, with very rare species, I use all specimens available.

I am fully aware of the inherent problems associated with attempts to characterize a much larger population with small samples: probability of obtaining abnormal means and/or standard deviations is high, especially if samples are drawn from a more extensive geographical area. Results from small samples increase the probability of sampling error. To decrease the probability of misinterpretation, I consider the general impression provided from statistics of other characteristics as evidence for probable internal contradictions, since it is very likely that some of the other characteristics will confirm a mean different from that of the total population; and it is unlikely that most other characteristics will show simultaneously abnormal results.

2.2.4 Illustrations

Line drawings were made with the aid of an ocular grid in a Leitz stereoscopic dissecting microscope, or from photographs. With complex structures, or surface microscopic features, I used photographs from the scanning electron microscope (SEM).

I provide maps of all North American species, and present a brief description of ranges of Euroasiatic species. Special maps were prepared to illustrate some clinal relationships, and to illustrate broad zoogeographic patterns.

2.2.5 Description Format

The description format I follow has been used previously by Ball (1966), Erwin (1968), and Whitehead (1971). For each taxon, I record the following: synonymic list; diagnostic combination; description; variation; linguistic roots of the accepted name; notes on habitat, life cycle, and behavior; and taxonomic notes. Under diagnostic combination and decription, each of the following life stages is treated separately; adult, and first, second, and third instar larvae. In the synonymic list, the following are included: valid name, synonyms and homonyms; and type (type species or specimens). Data in the decription are presented generally under the following headings: head, thorax, elytra, abdomen, wings, male genitalia, and ovipositor.

2.2.6 Taxonomic Method

2.2.6.1 Sorting of Taxa

Adults of Elaphrus were first sorted according to Lindroth's (1961) treatment of North American species. I followed the European traditional nomenclature with Euroasiatic species (especially Bänninger's identification).

Then, I arranged the material of these taxa geographically for a more refined intrapopulational analysis. To resolve problems of species recognition resulting from geographical variation, a preliminary study was undertaken to identify geographically variable characteristics. Data and statistics of dispersion were derived for samples of the material on hand yielding the best geographical coverage. I decided relationships and status of specimens within each species or complex on criteria given under species and subspecies in section 2.2. Application of names to North American taxa was based on personal examination of type specimens, or Lindroth's (1961) conclusions. For most Euroasiatic taxa, naming was based upon present tradition. Since Euroasiatic material was limited, I did not attempt any nomenclatural changes. Despite potential errors, I think that including information about these taxa provides a good basis for future studies of Euroasiatic members of the subgenus Elaphrus , and a better insight into the past history of the North American fauna.

Association of males and females of each species was easy as most specimens of most species occur in a special habitat or with individuals of distinctive species, and as males and females of a species are more similar to one another than to other species. Adults and immatures were associated by rearing from eggs (ex ovo) except for very distinct larvae of D. arctica and E. lapponicus.

2.2.6.2 Criteria for Species, Subspecies and Supra-Specific Taxa

Species are populations or groups of populations connected by actual or potential gene flow, but which are reproductively isolated from all other populations (Whitehead, 1971). The biological species concept is rarely tested in the field, for in most studies one deals with preserved specimens, and evidence for reproductive isolation is demonstrated by structural gaps. However, as a test for species established on the basis of structural features, in Alberta and at Inuvik, North West Territories, I observed carefully a few hundred matings in the field where two or more species of Elaphrus co-existed. I did not see hybrid matings, nor special segregation of color variety among mating pairs. Thus, the use of structural gaps in separating these sympatric taxa was supported by field observations.

However, presence of a structural gap is not necessarily conducive to recognition of two species, as a gene pool can include in one area more than one discrete variety i.e. most species of Elaphrus include two or three color varieties. Distribution and habitat of the varieties are clues for recognizing discrete intra-populational varieties. Two species very rarely show the same distribution pattern, but atypical variants are likely to show a similar pattern or be inside the geographical range of the common variety. It is unlikely also that two extremely closely related species live in exactly the same microhabitat at the same place, unless they are not competing for similar sources of food, but varieties of one species occur in a similar habitat and are likely to be associated. Combination of these two criteria and observation of mating interactions in the field helps to decide the status of these phena.

Recognition of sympatric species is generally relatively easy except for circles of races with terminal populations overlapping geographically. Evidence of reproductively isolated gene pools is provided mainly by structural gaps. For some species, adults are more divergent while for others larvae are. Therefore in studies related to definition of species or relationships between species, I use the total sum of characteristics of adults and immatures.

It is difficult to apply the biological species concept to allopatric phena. For these I compared first the degree of divergence observed among sympatric species pairs, and studied intrapopulational variation. If the interpopulational analysis suggested no gene flow and the structural gaps observed were similar to those observed among sympatric species pairs, I considered these two phena as separate species.

Subspecies are geographically delimited populations through which gene flow potentially or actually exists. (I discussed in section 2.2.6.3 approaches to recognizing evidence of gene flow among allopatric and parapatric phena.) Subspecies are populations in the process of speciation. I exclude from consideration intra-deme discrete variation, aberration, and any other variation. I also reject statistically insignificant divergence since it might result from adaptation to local short term selection agents rather than longer term evolution in isolation, or it might be simply the result of close interbreeding in small semi-isolated demes. I prefer multiple evidence as the basis for inferring that the phena have been isolated (with little or no gene flow) and are in the process of differentiating. Of importance in my work are behavioral and significant mean differences following principles outlined in section 2.2.6.3. Whitehead (1971) and Erwin (1967) among several authors suggested that if taxa of subspecific rank are to be recognized they should represent significant change in a gene pool.

I also apply the subspecies concept when in doubt about reproductive isolation of allopatric phena, following study of many structural characteristics. With most other geographical phena, where material was insufficient or where the divergence was less significant, I used vernacular names derived from area of origin (i.e., coastal form, Blue Mountain form etc.) to facilitate discussion. I hope such designations will encourage future students to investigate more thoroughly these geographical phena, and to demonstrate their status (species, subspecies, or not worth formalizing). I do not find this subspecies concept undesirable. Significant gene pool change is of value to students of faunistics and evolution, and such forms should have formal names.

Supra-specific taxa are defined as groups of one or more species separated from other such groups by a clear gap. This definition is arbitrary as to inclusion and results in nomenclatural instability (Simpson, 1961). In my work the only condition I tried to satisfy was monophyly or naturalness. I accepted the established concept of Elaphrus and four of its presently defined subgenera. I have no doubt about their naturalness. I also accepted the other groups of Elaphrini that are ranked as genera.

2.2.6.3 Analysis of Geographic Variation

If means of two samples differed from each other by two standard errors in one or more characteristics, I took it as evidence of evolutionary divergence. Indeed, no two populations are exactly alike since evolutionary pressures vary in time and space. Isolation, time and selective pressures affect the extent of evolutionary change. At the extreme, speciation occurs when two populations have diverged sufficiently to be reproductively isolated, and have lost reproductive links with other populations.

Statistically different means between proximate samples suggest divergence, but study of means of intermediate populations provides evidence about gene flow between the first two populations. If the nearest populations of two allopatric phena are the most similar, or show at least no sign of divergence among characteristics studied, I concluded that gene flow potentially or actually existed, and thus these populations were conspecific. If these two populations were most divergent, or at least divergent in one or preferably most characteristics, I concluded that gene flow was unlikely to exist now between these populations, and thus they were not conspecific (character displacement). However, if these two populations show evidence of gene flow between intermediate populations (as in circle of races) even if these populations are reproductively isolated (as demonstrated in parapatric or sympatric situations), I considered them conspecific.

Like Whitehead (1971), I found that the most meaningful statistical approach was to compare means of proximate samples rather than other statistical parameters. These statistics suggest whether differences between means are or are not results of coincidence. For example, if two samples differed significantly in their means in one characteristic, but an intermediate sample differed from neither, I concluded not only that the first two samples had diverged, but also that gene flow continued between them. If these statistics represent quite closely the reality in field populations, I think the pattern is unlikely to result from chance.

2.2.6.4 Classification of Taxa

Systematics makes its ultimate explanation as the development of evolutionary theory. A cladogram and its resulting classification provides an hypothesis about evolutionary relationships between taxa (see section 4.0). It makes predictions about other systems of reference: biochemical, behavioral, chromosomal, and larval. It infers important evidence of past zoogeographical events. Finally, it shows, if desired, the degree of divergence between taxa (Ashlock, 1975). Phenograms illustrate the relative divergence between taxa. However, if they are used as a means of reconstructing phylogenies, then the hypothesized phylogeny and resulting classification lacks a theoretical base as the phenogram measures divergence which is affected by time and rate of change, and therefore is not evidence for propinquity of descent, and is more likely to lack the predictability of the above approach (see section 4.0). In this work I tested independently for congruency two reference systems (adult and larval classifications) using cladistic and numerical principles. Principles and methods are more fully discussed in section 5.0.

3.0 Classification

3.1 Tribe Elaphrini

Adults. Diagnostic combination.- Antennomeres 3 to 11 or 4 to 11 pubescent; supraorbital setae two pairs; in most species medial tooth of mentum deeply emarginate; pronotum with two pairs lateral setae or with one pair near middle; forecoxal cavities closed behind; midcoxal cavities disjunct; mesosternum with two convergent ridges anteromedially; metasternum with V-shaped micropunctate or punctate impression medially; metepimeron very narrow (in some specimens fused to metepisternum); stria 5 deeply impressed basally, or stria indistinct, area impressed and punctate; umbilicate series uninterrupted; lateral ridge under elytron with apical stridulatory file of longitudinally oriented keel-like sculpture; foretibia with dense fringe anteriorly (Fig. 145); tarsomeres 1 to 4 or 1 to 3 of foreleg enlarged with spongy pubescence ventrally; internal apical angle of midtibia of males of most species protruded into small point (Fig. 150); tergum 7 with lateral pair of plates expanded apically into curved row of points--stridulatory scraper; sterna 4, 5 and 6 of abdomen each with transverse basal stria; male median lobe with aperture of internal sac dorso-subapically; basal part of internal sac extended posteriorly through basal orifice formed by fusion of three sclerites around ejaculatory duct (Fig. 39) into large stylet, sac partially eversible and covered with modified alveolae of microsculpture (setae, small and large scales, and microtrichia); lateral lobes of male genitalia subequal in length, right lobe 1.3 to 2 times as wide as left lobe, ventrally both with dense long fringe (Fig. 53b and 53c); basal sclerites of stylus of female genitalia with setae or spinules dorsally and/or apically (Fig. 70-75).

Adults. Description.- Medium to large (length of body 6.0 to 18.0 mm). Body elongate, with head, pronotum and elytra clearly delineated. Color of dorsum black or with copper or green metallic reflections. Integument shiny or dull; microsculpture varied in extent, alveolae isodiametric generally, but in areas transverse. Pore in punctures small or in one member large.

Head. Average for carabids, eyes prominent or not. Mouthparts prognathous or hypognathous. Anterior margin of labrum straight or slightly convex; dorsal surface with six anterior setae and ventro-laterally with six or seven pairs of short, curved setae. Clypeus with two latero-basal or with two more medial setae; surface impunctate or punctate to different extent; clypeal suture evident. Dorsal surface of head capsule densely punctate, less so laterally, or impunctate; antero-lateral impression of frons indistinct or sharply outlined with octagonal impressions; two pairs of supraorbital setigerous punctures; discal impression absent or present; members of most species with weak transverse impression behind eyes; side of head capsule with semi circular bead; neck not narrowed. Antennal scape with one antero-dorsal seta; antennomere 2 glabrous or with one or two setae; antennomere 3 partly pubescent, plurisetose, or with few apical short setae; antennomeres 3 to 11 or 4 to 11 pubescent; antennomeres 3 to 11 moderately transverse (1.8 to 2.5 longer than wide); no ridges or beads on antennomeres.

Mouthparts. Mandibles of average shape for carabids (Fig. 1-34); each with one seta dorso-laterally in anterior third of mandibular scrobe, and without rugae or sulci dorsally; left mandible with sharp long terebral cutting edge ended basally as terebral tooth, below with retinacular ridge slightly protruded basally as retinacular tooth, below basally with sharp molar tooth; ventral brush average; right mandible as above except retinacular ridge with an anterior retinacular tooth, or with third retinacular tooth. Right mandibular cutting edge 0.5 to 0.7 and left one 0.2 to 0.25 of total length; mandibular teeth about equidistant from each other. Maxilla (Fig. 5). Lacinia with two rows of spinules (8 to 13) along internal margin; spinules 1.0 to 1.2 length of lacinia width; lacinia apex acute, generally abruptly bent into tooth; tooth 1.0 to 1.5 length of lacinia width; few setae dorso-basally, ventro-internal 0.5 with setae and small pores, setae denser and longer basally. Galeomere 1 with two large dorso-apical pores, 1.5 to 2.0 length of galeomere 2, and 1.0 to 1.5 length of maxillary palpomere 2; galeomere 2 with one dorso-apical large pore and many small pores and apex acute; galeomeres slender; stipes external margin with three setae in basal 0.5, antero-dorsal internal angle with small field of pores, ventral surface with indistinct to convex alveolae of microsculpture, and with few small pores. Palpifer with two to four setae on external margin; palpomere 1 with two subapico-ventral, two subapico-dorsal large pores and with small field of micropores externo-basally; palpomere 2 with two subapical dorso-internal and one subapical dorso-external large pores; palpomere 3 with one subapical ventro-internal large pore and few subapical pores, palpomere 4 with one subapico-external large pore and many small pores in apical 0.67; palpomere 1 0.4 to 0.5 length of palpomere 2; palpomere 2 1.5 to 1.75 length of palpomere 3; palpomere 3 0.5 to 1.0 length of palpomere 4; palpomere 2 as narrow as or wider than other palpomeres, otherwise palpomeres slender; palpomere 2 and, in most members, all palpomeres with indistinct meshes of microsculpture. Labium (Fig. 8). Ligula much or little projected; with two subapical proximate setae and few small pores; paraglossae narrow, serrated on internal margin, and usually projected beyond ligula apex. Palpiger with one small ventro-basal seta; labial palpomere 1 with two dorsal and two ventral large pores; palpomere 2 with one apical large pore, many small pores and two setae; palpomere 3 with one apical large pore and numerous small pores; microsculpture of palpomeres indistinct. Mentum average; anterior emargination in depth

0.33 of mentum maximum length; medial projection in form of bicuspid tooth; tooth length 0.5 to 0.75 of mentum emargination depth, tooth emargination 0.2 to 0.75 of tooth length; anterior angles of lobes in most members projected and acute; disc of mentum with two medial setae or with two more setae latero-basally; microsculpture indistinct to convex on lobe with 10 to 30 small pores. Submentum with six or eight setae, and in some members with few accessory very small setae; microsculpture alveolae indistinct to convex; gula minimal width about 0.3 submentum maximum width, without or with microsculpture alveolae in narrowest part, followed by indistinct slightly transverse alveolae, and terminated near base of head with convex alveolae in form of short scales with elevated margin point forward, alveolae front margin with 0 to 3 microteeth.

Thorax. Pronotum wide to narrow; lateral margin explanate, narrow, or pronotal epipleuron and disc of pronotum fused smoothly along length of margin or part of it; disc with two pairs of lateral setae, with one pair near hind angle, or without setae; in some members disc with few scattered fine setae; anterior and posterior fringe extended or not to postero-lateral angles, setae of fringe narrow or scimitar-shaped, in most members fringe setae shorter near middle of margin; punctures extended laterally and basally on disc, puncture 18 to 40 microns in size, punctures 0 to 600 microns apart, puncture distribution quite uniform or spotty, edge of punctures sharply outlined on 30% of circumference; surface without or with lines, and without or with mirrors; discal impression absent or one to five on each side; microsculpture lines evident in most members at least in baso-lateral impression; lines on disc indistinct, alveolae flat or convex, in areas alveolae differently expressed in some members .

Proepipleuron wide or narrow, in most members wider near base or near middle, without or with punctures. Proepimeron with postero-longitudinal ridge; proepimeron fused to proepisternum or suture well defined; punctures absent or present, puncture 20 to 40 microns in size, punctures 0 to 400 microns apart, edge of each puncture sharply outlined on 30 to 100% of circumference; microsculpture line absent or evident, alveolae flat to convex, on disc isodiametric and basally slightly transverse.

Proepisternum (Fig. 107 and 109) with complete or incomplete sulcus between internal flange and external episternum near junction with proepipleuron, flange small to large relative to episternum size; punctures absent, or present, puncture 15 to 40 microns in size, punctures 0 to 160 microns apart, edge of puncture indistinctly or sharply outlined up to 100% of circumference; microsculpture lines absent or present, alveolae flat to convex. Prosternum average; lateral suture with proepisternum slightly sinuate or sharply angulate; fringe of setae along anterior margin, setae normal or scimitar-shaped, in most members shorter near middle of margin; surface punctate, or impunctate, puncture 15 to 40 microns in size, punctures laterally to 400 microns apart, edge of punctures indistinctly or sharply outlined up to 100% of circumference; setae present or absent from process or disc; microsculpture lines absent or present, alveolae flat to convex, in most members more convex laterally, on disc alveolae partly or generally slightly transverse, alveolae on coxal cavities single-pointed and directed outward, pointed sculpture small or larger.

Scutellum; basal transverse sulcus outlined or absent, lateral ridge extended nearly to apex or not; punctures baso-medially or on surface, puncture size 20 to 30 microns, punctures in contact or up to 300 microns apart, edge of puncture sharply outlined on 30 to 75% of circumference; pores in punctures small in all members; microsculpture lines absent or present, alveolae flat to convex, best expressed at base where in most members partly or mostly slightly transverse, isodiametric in apical 0.5.

Mesepimeron narrow especially near coxa of midleg; punctures absent or present, puncture size 20 to 45 microns, punctures in contact or up to 450 microns apart, edge of punctures indistinctly or sharply outlined up to 70% of circumference; microsculpture alveolae convex to absent. Mesepisternum with slightly sinuate ridge near basal margin, discal ridge (curved forward) present, indistinctly outlined or absent, punctures absent or present; punctures 20 to 45 microns, punctures in contact or up to 180 microns apart, edge of punctures sharply outlined on 0 to 70% of circumference; microsculpture lines absent or present, alveolae flat to convex, alveolae anterior to discal ridge partly or totally slightly transverse, area between basal margin and basal ridge without meshes.

Mesosternum; postero-lateral ridge developed, suggested or absent, baso-medial area with two convergent ill-defined ridges; process without or with setae; punctures absent or present at least postero-laterally, in some members, punctures expanded on surface except at base, puncture size 25 to 45 microns, punctures in contact to 280 microns apart, edge of puncture sharply outlined over 0 to 75% of circumference; microsculpture lines absent or present, alveolae flat to convex, in areas scale-shaped without or with microteeth on medial areas, in few members extended laterally, or expanded into point at base, alveolae slightly transverse baso-medially and in part laterally.

Metanotum; with two fields of setae, one latero-posteriorly and one latero-medially; postero-lateral setae short or long, medio-lateral setae few or numerous. Metepimeron very narrow, in most members separated by suture from metepisternum; L-shaped sclerite posterior to epimeron narrow and not visible externally; membrane behind L-shaped sclerite with field of small setae. Metepisternum 1.5 to 2.5 longer than wide; anterior sulcus absent, indistinct or well defined; antero-dorsal membrane (hidden under elytral epipleuron) with field of few or numerous short setae; ridge in postero-dorsal 0.5 well defined and hidden under elytral epipleuron; disc without or with setae; punctures absent or present, punctures 15 to 40 microns, punctures 10 to 100 microns apart edge of puncture sharply outlined on 50 to 70% of circumference; microsculpture lines absent or present, alveolae absent to convex.

Metasternum average; medial-anterior process with sulcus, or without; medial inverted V-shaped area defined by pores or punctures; punctures absent or present laterally and on V-shaped area, punctures 20 to 40 microns, punctures laterally 0 to 250 microns and in V-shaped area 0 to 400 microns apart, laterally 0 to 90% and medially 20 to 100% of punctures with setae; microsculpture alveolae absent to convex, more convex laterally, in most members isodiametric laterally and slightly transverse medially.

Elytra. Elytral proportions average or shorter; nine striae clearly outlined at least on disc or absent, or intervals between striae 7 and 9 ill-defined, base of stria 5 more deeply or slightly impressed basally; basal projection at junction of elytron and mesonotum with two to seven oval punctures; transverse basal stria complete, extended only to fifth stria, or to humerus; six to 10 setigerous punctures along umbilicate series, series not interrupted; disc with one scutellar setigerous puncture, with setigerous punctures on third, third and fifth, or third, fifth, and seventh intervals; third interval with five to seven setigerous punctures, fifth interval with two to four setigerous punctures, and seventh interval with four setigerous punctures. Striae straight, or convergent toward setigerous punctures (Fig. 28); striae not in contact or in contact posterior to setigerous punctures (Fig. 30), or striae in contact anterior to setigerous punctures, extended around and in contact posterior to setigerous punctures (Fig. 29); striae distinct or indistinct but around setigerous puncture as above (enclosed area around setigerous puncture is termed "pit") (Fig. 31). Pits clearly outlined and setigerous except for two non-setigerous pits at base of elytron near position of intervals 5 and 7; umbilicate setigerous punctures with pit; setigerous punctures very large or small; elytron with reflective surface (termed "mirror") anterior and/or posterior to pits or absent (Fig. 112-117); elytron with one to 15 mirrors; punctures restricted to striae where defined, four to 200 punctures per pit, puncture size 20 to 45 microns, punctures in striae 90 to 120 microns apart, in interval in contact to absent, in pit in contact to 40 microns apart, edge of punctures in most members indistinctly outlined or sharply outlined on 50 to 100% of circumference; pores few or very numerous; microsculpture lines present, alveolae flat to convex apically, lines absent or present on intervals, and mirrors without or with indistinct lines, alveolae flat to convex on interval.

Elytral epipleuron impunctate or with punctures;

puncture size 25 to 40 microns, punctures in contact to 150 microns apart, edge of punctures indistinctly outlined or sharply outlined up to 40% of circumference. Elytral ventral surface with stridulatory file subapically along internal ridge; microsculpture lines absent, file sculpture formed of longitudinally elongate microridges; apical two-thirds of disc sculpture formed of trichia, and elytral internal ridge sculpture formed of erect microscales.

Wings. Very similar among genera (Fig. 32). Posterior end of oblongum rounded or subangular.

Abdomen. Abdominal terga average for carabids; stidulatory scraper plate laterally on tergum 8, plate widened postero-medially; postero-medial margin of plate with 11 to 25 sharp points; tergum 1 with about 100 setae or absent from middle, or without setae; terga 2, 3, 4 and 5 without setae or laterally with few pores; tergum 6 with two microtrichial fields basally on both sides of middle, tergum 7 with microtrichia as on tergum 6 but extended to posterior margin; scraper plates with about 30 setae of different lengths; setae restricted to or expanded from plates along basal margin as one row, or setae on tergum 7, tergum 8 with setae on most of surface; setal size different among members; tergum 2 with or without two transversely arranged short sclerotized ridges medio-anteriorly; microsculpture lines absent or present, alveolae on stridulatory scraper plates, along mid-rib of terga 2, 3, 4, 5 and 6, and on tergum 8 alveolae convex to flat, or absent.

Abdominal sterna 5 and 6 with transverse basal sulcus; one pair of large medial setae on sterna 4, 5 and 6, sternum 7 with one or two pairs of postero-marginal setae; disc of sterna 4, 5 and 6 each with accessory setae in some members: sternum 4 with 15 to 40 setae, sterna 5 and 6 each with 10 to 100 setae or without or with one or two setae, sternum 7 without setae or with 10 to 100 setae; accessory setae expanded laterally near margin or not, setae less numerous in females or similar between sexes; punctures absent or present laterally, or laterally and on disc of sternum 2, or on sternum 3, or on disc and laterally on sternum 4, or on whole of sternum 2 and laterally on sterna 3, 4, 5 and 6, and in most members on sternum 7; puncture size 25 to 40 microns, punctures in contact or to 150 microns apart, edge of punctures sharply outlined on 50 to 70% of circumference; microsculpture lines absent or present, alveolae flat to convex, more impressed laterally, and slightly transverse medially in most members.

Legs. Forelegs anisochaetous (Fig. 145 and 146); coxa globose; punctures absent or present; puncture size 15 to 30 microns, punctures 10 to 300 microns apart, edge of puncture sharply outlined on 30 to 50% of circumference; microsculpture lines at least in spots, alveolae flat. Trochanter with one, two, or three setae; microsculpture lines absent or present, in some members difficult to see, alveolae flat. Femur internal margin without or with large sharp projection; surface with 12 to 18 setae, or with three or more times as many; six or less setal rows indistinctly outlined (two or three anterior and three posterior), or with nine rows (four anterior and five posterior); microsculpture lines absent or present, alveolae flat or convex, in some members slightly transverse. Tibia close to grade B type (for terms see Hlavac, 1971), i.e. setal band long with vertical section, setal band about 30% of tibia length, medial expansion present but not shifted far anteriorly; antennal channel shallow and developed far posteriorly to clip setae; different from grade B type in lacking confluent zone between setal band and anterior internal fringe (ASR in Hlavac, 1971); without or with projections at base of spurs, or with one near posterior spur; posterior spur about half way between apex of antennal cleaner and basal clip setae, or very close to clip setae; clip setae curved but not sinuate; surface with five rows of fine setae or spinules extended partially or totally along tibia; excluding anterior internal fringe tibia with about 25 setae, or at least twice as many in some members; anterior internal fringe very dense extended along apical third or extended over apical 0.5 to 0.67; one pair of large pores on anterior and posterior side at base; microsculpture lines absent or present, alveolae flat to convex, or scale-like, alveolae better expressed in apical third. Tarsomeres 1 to 3 or 1 to 4 of males enlarged or slightly enlarged and with spongy pubescence ventrally, or narrow and without pubescence; tarsomere 1, 2, 3 and 4 each with four to eight spinules ventrally, or with 10; microsculpture lines absent or present, alveolae flat or convex.

Midleg average (Fig. 147 and 148). Coxa with one, two or numerous setae; punctures absent or present, puncture size 20 to 30 microns, punctures 25 to 200 microns apart, edge of puncture sharply outlined over 30 to 50% of circumference; pores small or large; microsculpture lines absent or present, alveolae flat to convex, in most members with slightly transverse alveolae. Trochanter without or with one, two, or three setae; microsculpture lines absent or present (difficult to trace in some members), alveolae flat, alveolae in part slightly transverse. Femur ventral margin normal or angulate; femur with four to six rows of setae (one to four anteriorly, two or three posteriorly), or with 10 rows; femur with 15 to 25 setae or with twice as many; microsculpture lines absent or present, alveolae flat to convex, alveolae slightly transverse in few members. Tibia with interno-apical projection at base of anterior spur in males of most species; surface with five rows of setae, only two rows not extended to base: one behind apical fringe, and anterior dorso-lateral row; posterior apical fringe extended on anterior side internally to 15 to 100% of tibia length; anterior dorsal row with setae arising from small elongate ridges; posterior dorsal row ridges more developed and interconnected; rows formed of one line of setae, or apical third or fourth of anterior dorsal, posterior dorsal and posterior ventral rows expanded; tibia with about 40 setae or with about twice as many; microsculpture lines absent or present, alveolae flat to convex, often scale-shaped, best expressed apically. Tarsomeres 1, 2, 3 and 4 each with four to eight ventral spinules, or with 10 or more, tarsomeres with two to six ventral setae or 10; microsculpture lines present, alveolae flat or convex.

Hind leg average. Coxa medially with one major seta and with three to 40 smaller setae, these setae distributed on or restricted internally; punctures absent or present; puncture distribution on or divided into two groups; some or all punctures with setae; puncture size 20 to 30 microns, punctures in contact or up to 200 microns apart, edge of puncture poorly defined or sharply defined up to 70% of circumference; small circle of five to 10 pores in small depression hidden postero-medially; large or shorter apodeme projecting anteriorly; pores small or large; microsculpture lines present (in some members difficult to trace), alveolae flat. Trochanter with about six spinules on posterior side at base or with twice as many; microsculpture lines present, alveolae flat and in part slightly transverse. Femur with half dozen setae, or with twice or more as many setae distributed on six rows; microsculpture lines absent or present, alveolae flat to convex, best expressed toward apex. Tibia with four rows of spinules or with fifth dorsal row; row formed of single line of setae or with posterior and anterior rows expanded in apical third or fourth into field of setae; tibia with about 40 setae or twice or more as many; microsculpture lines present, alveolae flat, or convex, alveolae better expressed apically. Tarsomeres 1, 2, 3 and 4 each with four to 12 setae or with about 24; microsculpture lines present, alveolae flat or convex.

Male genitalia. Median lobe (Fig. 38); dorsally thinly sclerotized or quite thickly sclerotized, ventrally and baso-laterally thickly sclerotized or less distinctly from dorsal surface; parameres subequal, paramere 0.5 or about as long as lobe, left paramere wider than right; ventral margin with setae (two rows) extended from apex but not reaching base; setae long or short and similar in length on both parameres; apex of lobe in most members spatulate, or apex in lateral view with a large or small dorsal and with or without large or very small ventral point; shape of spatula different in most members; basal two-thirds of lobe tube-like tapered down toward apex, or constricted ventrally near basal orifice; internal sac opening dorso-subapical; sac apical portion easily eversible; interior of sac with microtrichia, brushes, fields of scales; posterior portion of sac extended posteriorly well past basal orifice as stylet, stylet formed of three sclerites surrounding ejaculatory duct, ejaculatory duct entering stylet sub-posteriorly, stylet closely attached to cup-shaped sclerite at base of internal sac.

Ovipositor. Average (Fig. 70); tergum 10 with numerous setae, tergum 9 and valvifer with sparse setae, or very few setae; setae moderate, small, or very small. Stylus formed of two sclerites, basal sclerite with setae around dorsolateral ridges, or on apical 0.2 or 0.67; setae fine or spinulose; apical sclerites without or with one or two apical setae; side of apical sclerite with few small scattered setae, or with two to six stout lateral spines, or without setae; microsculpture lines absent; internal structures of ovipositor not studied in detail, sclerites when present indistinctly outlined.

First Instar Larvae. Diagnostic combination.- Campodeiform. Head not constricted at base, neck defined laterally by shallow emargination of lateral margin; cervical groove, ventro-lateral sulci, supraocular and postero-ocular sulci absent; nasale projected medially as wedge, adnasale projection posterior or levelled with nasale projection; egg-bursters present; epicranial suture present. Antennae as short as mandibles with four antennomeres; antennomere 3 with large sensory appendage; antennae inserted more laterad than base of mandibles. Mandible with penicillus baso-internally and small seta on external margin level with retinaculum; cutting edge of retinaculum and/or cutting edge above retinaculum without or with fine teeth. Lacinia on stipes coniform or very little projected; lacinia with small apical or extremely small subapical seta; palpomere 3 shorter than two preceding ones. Prementum with prominent ligula though collapsed in some individuals;

labial palpomeres subequal in length, palpomere 2 fusiform. Terga small, epipleurites visible from above; terga distinctly outlined, without anterior and lateral bead, and slightly tapered toward apex; terga 1 - 8 divided medially by suture, terga 9 and 10 fused; urigomphus on tergum 9 unjointed, unarticulated, leathery, relatively slender, about as long as tergum 10, and with one weak medio-external nodule; urogomphus with five major setae and one very small seta; pleural sclerites short, about half segment length; sternites clearly separated from each other by membranous surfaces; empodial setae between claws absent.

First Instar Larvae. Description.- Small to medium, body length about 4 - 8 mm. Body campodeiform and cylindrical. Color pattern various on head, thorax and terga darker, urogomphus dark or pale, pleural and sternal surfaces testaceous or very light gray. Integument shiny or dull, sculpture on most sclerites pointed or sculpture absent.

Head. Frontale average (Fig. 87 to 92) dark or pale; egg-bursters baso-lateral, parallel, black, keel-shaped and extended below level of EM-P; nasale medial point level with or projected beyond adnasale; teeth on nasale absent or present; teeth very small to very large, and extended to medial projection or widely separated by medial projection; adnasale projected moderately or slightly; frontale suture bisinuate; frontal surface uneven, highest point at middle of disc; pore MMP-E internal to apex of egg-bursters or external, pore MA-I parallel or internal to seta MMA, seta EA-E virtually absent to medium-small, setae EMP and MP virtually absent to small, otherwise setae size and position as illustrated; microsculpture lines absent from most of surface, alveolae absent or weakly impressed antero-medially, alveolae absent or scale-shaped latero-basally on both sides of egg-bursters.

Dorsum of parietale (Fig. 87 to 92) testaceous, or testaceous except for darker proximal frontal suture area, or testaceous laterally, or at base and behind eyes, or at base only; ventral surface testaceous or pale at base only; head elongation average, convexities of lateral margin anterior and posterior to neck subequal or anterior convexity about 0.5 length of posterior one, epicranial suture as long as scape or as short as 0.2 of scape length; eye with six ocelli; head proportions defined by following ratios (Fig. 77): dorsally- FW/ES 3.3 to 12.0, PL/ES 3.0 to 9.6, FL/ES 2.4 to 9.2 PL/ES 4.0 to 6.2, Pl/PL 1.4 to 5.2, FW/PL 1.0 to 1.6, PLP/PlP 1.8 to 5.5, PW/PLP 1.6 to 2.5; ventrally- PML/PBW 0.7 to 1.2, PW/PML 1.1 to 1.8, PlP/PlA 2.2 to 14.0; seta DEP size medium to large, setae DMM-A, DMP-A and VEM-P size small to medium, setae DI-A and VMA size medium-small to large, setae VEP-P and VMP-A size medium-small to very large; seta DI-A slightly anterior to frontale postero-lateral angle or nearly level with it; angle formed by seta DI-A and pores DI-P and DMP-E from about 170° to 90°; pore VEP-A external or internal to seta

VEP-P, DMM system with DMM-P about level with frontal postero-lateral angle or anterior, VEM-P and VEM-A closed or distant--VEM-A posterior to or level with ventral posterior ocellus; meshes of microsculpture absent or present, alveolae flat to convex dorsally; meshes extended on most of dorsal surface, or laterally, or baso-laterally.

Antenna with four antennomeres; antennomere 3 0.7 or 1.5 as long as antennomere 2, antennal scape equal or 1.2 as long as antennomere 2, antennomere 4 0.7 as long as antennomere 3; scape with two ventro-medial, one ventro-subapical, and one dorso-apical large pore; antennomere 2 with externo-medial pore; antennomere 3 with large externo-apical sensory appendage, with small dorsal sensory appendage posteriorly, with one externo-subapical, one interno-apical and one dorsal baso-medial medium-small seta, with large pore posterior to dorsal baso-medial seta, antennomere 4 with three apical small sensory appendages closely associated with one very small seta, with two small setae subapically, and one dorso-medial small seta with large pore posteriorly.

Mouthparts. Average. Mandibles sickle-shaped with well-developed retinaculum; base of mandible posterior to retinaculum, narrow (internal margin apparently continuous with apical internal margin) or wider; retinaculum posterior margin and/or apical cutting edge toothed or not, teeth very fine or larger; penicillus present baso-internally along margin, penicillus formed by four to seven closely associated small setae; external margin at level of posterior margin of retinaculum with small seta and one large pore behind; medial surface of mandible with one medio-subapical and one medio-subbasal pore; sculpture absent. Maxilla--cardo narrow with medium-small seta near external margin; no sculpture; stipes (Fig. 83) two to five times as long as wide; external margin with two large setae, one in anterior and one in posterior 0.33, anterior seta lower or above level of seta posterior to lacinia; small seta posterior to lacinia on internal margin; internal half of dorsal surface with about 30 to 50 setae in basal 0.66, those in apical 0.3 distributed in one or more rows; one small seta ventrally near margin posterior to lacinia; stipes with three pores ventrally: one posterior to palpus, one medially in basal 0.33, and one more basally medio-externally, medial pore anterior or nearly level with posterior postero-external pore (thus pores close or far apart); ventral surface darkly tanned or behind posterior seta on external margin thinly sclerotized without or with lateral extrusion; microsculpture lines absent, sculpture pointed on most of dorso-external 0.5 of disc. Maxillary palpus formed by articulated palpifer and three palpomeres; palpomere 2 subequal or 1.5 length of palpomere 1, palpomere 1 about twice length of palpifer, palpomere 3 0.5 to 0.7 length of palpomere 2; palpifer with small ventro-medial seta; palpomere 1 with two large ventro-subapical pores; palpomere 2 with one large and one small pore dorsoapically; palpomere 3 with few small pores, elongate subapical sensors and apical microsensors; no sculpture. Galea with two subequal galeomeres: galeomere 1 with very small or small ventro-subapical seta, galeomere 2 with one interno-basal and one internal microseta in basal 0.33 to subapex; no sculpture. Lacinia cone-shaped or barely suggested; seta on lacinia small or barely visible, small seta apical but microseta subapical, lacinia seta about as large or 0.1 length of seta posterior to lacinia on stipes; no sculpture. Labium (Fig. 82) with prominent (in some specimens collapsed) ligula; ligula with two small proximal setae. Prementum dorsally on each side with one very small seta latero-subapically, and medium-small seta medio-laterally; ventrally with one very small seta baso-sublaterally, and one large pore subapically near middle; ventral surface darkly tanned and dorsal surface tanned antero-laterally; microsculpture lines absent, sculpture present on thinly sclerotized dorsal surface as wide points. Labial palpus with two subequal palpomeres; palpomere 2 confusiform; palpomere 1 with ventro-subapical large pore, palpomere 2 with few small pores over surface, with field of elongate sensors baso-externally, and microsensors apically; no sculpture. Mentum thinly sclerotized without sculpture.

Thorax. Pronotum (Fig. 76c) extended over most of dorsum of prothorax and laterally over dorsal part of pleuron; pronotum with medial sulcus; disc darkly sclerotized, and pronotal epipleuron anterior and posterior bands thinly sclerotized, anterior band pronotal epipleuron sharply separated from disc, but posterior band diffusely separated, anterior and posterior bands and basal part of pronotal epipleuron with vermiculate black pigment, anterior bands with irregular longitudinal channels; edge of disc without bead; origin of indistinct sulcus lateral on disc in apical 0.33 and extended inward for short distance near level of ME system; each side of pronotum with three rows of setae, anterior row with four setae and one pore, middle row with one pore and two setae and posterior row with five setae and five pores; seta and pore position and size of setae similar among members except in following: seta AII-E size small to large, setae MI and ME-I size small to medium, seta PII-P very small to medium-small; microsculpture lines present or absent from disc, absent from bands and pronotal epipleuron; brown pattern areas indistinctly outlined, lines transverse not forming alveolae; unpatterned surface without or with alveolae extended on disc in some members, alveolae isodiametric or scale-shaped on up to about 30% of surface. Proepisternum with seta antero-dorsally, antero-dorsal seta very small to medium; no sculpture. Proepimeron with seta medially; seta very small to medium; no sculpture. Prosternite darkly sclerotized with anterior 0.5 thinly sclerotized as on pronotum anterior band; posterior band with two to three pores; disc with postero-medial pair of setae and about five to seven pairs of pores sublaterally; no sculpture. Poststernite with seta; setae virtually absent to small; anterior legs separated from posterior disc.

Mesonotum average (Fig. 76c); shorter than pronotum; medial suture present; lateral transverse sulcus absent; anterior margin beaded; mesonotal epipleuron and posterior band as pronotum anterior band thinly sclerotized, no anterior band; mesonotal epipleuron distinct from disc, and posterior band diffusely distinct from it; behind anterior margin of disc with submedial group of two setae and one large pore (BI) and sublateral group of three very small setae (BE); posteriorly setae on disc similar to pronotum except systems AII and AIM without pores, systems MI and ME absent, seta PEP-P and pore PEM-A absent; seta AIM and AIE-I small to large, setae PMI-I and PIE-A small to very large, seta PII-P very small to medium; microsculpture lines absent or present, alveolae, excluding brown patterned surface, over 10 to 70% of surface, alveolae shaped as sharp scales absent or laterally up to 30% of surface, mostly laterally, and near suture up to 5% of surface; posterior band without sculpture or with micropoints extended up to 100% of surface. Mesepipleuron seta small to very large; no sculpture. Sternite with pair of setae; seta medium-small to large. Metathorax similar to mesothorax except sculpture, in some members, slightly more expanded, and anterior margin not beaded.

Membranes between sclerites without alveolae, sculpture pointed; micropoints barely visible postero-laterally on dorsum, laterally on pleural surface extended on 40 to 90%, and ventrally over 20 to 90% of surface; micropoint pattern different between most members; micropoints very small or large.

Abdomen. Terga (Fig. 76e) with medial suture, except terga 9 and 10 entire; terga widest anteriorly, maximum width for each tergum tapering toward tergum 9, tergum 10 narrower; tergum 9 with pair of urogomphi as long as tergum 10, urogomphi unarticulated, unjointed, moderately slender, leathery with small knob externally near middle, and in dorsal view curved inward (Fig. 93a, 95, and 98a) tergum 10 with two posterior pairs of eversible sacs (one dorso-medial and one ventro-lateral pair) covered with small hook-shaped crochets; terga 1 to 10 without defined anterior band and tergal epipleuron; posterior band indistinctly separated from disc and more thinly sclerotized, posterior band with vermiculate black pigment and without irregular longitudinal channels, tergum 10 without posterior band; setae on terga 1 to 8 similar in composition and distribution to mesonotum and metanotum except setae BI-A, pore AE-P, and systems AIE and PE absent (setae on tergum 9 and 10 not homologized), setae BE-A and BE-P present on tergum 1 only; setae AII and AIM small to medium, in some members seta AIM much smaller on any terga of terga 5 to 8, seta PII-P very small to medium-small; microsculpture lines absent or present, brown patterned surfaces as for pronotum; sculpture in posterior 0.5 of terga single-pointed, in anterior half of disc alveolae multi-pointed; sculpture on disc of tergum 1 in many members more restricted; anterior band without sculpture; sculpture on tergum 10 single-pointed or multi-pointed; sculpture on urogomphus single-pointed, broad scales, or raised part of scale irregular and crenulate; sculpture in apical 0.5 of urogomphus indistinct or absent. Abdominal epipleuron (Fig. 76f) seta Ep-A very small to medium, on segments 2 to 5 seta Ep-A small to large, on segment 9 smaller in all members, or Ep-A smaller on any of segments 1 to 8; microsculpture lines absent, sculpture absent or with very fine scattered points. Hypopleuron present on segments 1 to 8, fused to sternum on segment 9 and absent from 10; without setae or pores; microsculpture lines and sculpture absent. Abdominal anterior sternite (AS) very small with one very small seta, anterior sternite fused to sternum 9 and absent from sternum 10. Abdominal sternite large without medial suture, fused to other sternites on sterna 8, 9 and 10; sternite on segments 1 to 8 with one pair of setae, and absent from sternum 9 (setae on sternum 10 not homologized); seta of sternite 2 medium to medium-small; no sculpture. Internal poststernite with two setae; seta PsI-E size very large and seta PsI-I size on segments 1 to 9 very small to medium-small, or on segment 9 in some members larger than on segments 1 to 8; no sculpture. External poststernite with two setae except on segment 1 with PsE-A only; seta PsE-P size on segments 2 to 9 large, seta PsE-A on segments 1 to 8 medium-small to medium, on segment 9 small to medium-large; no sculpture.

Membrane microsculpture without lines, sculpture absent or present in spots, sculpture pointed, points virtually absent, small or larger; sculpture expanded dorsally behind tergum, on pleural surface very restricted, or extended on most of it, and on sternal surface restricted or expanded on most of it.

Legs. Very similar between segments of thorax and between members. Anterior face of coxa studied, remaining not studied in detail. Setae on coxa as illustrated; microsculpture lines absent, sculpture of fine sharp scales, or absent. Trochanter with one interno-apical and one interno-medial seta, with two large pores medially on anterior side and two pairs of apical spinules on anterior and posterior sides; no sculpture. Femur with one baso-external very small seta, two pairs of apical spinules on anterior and posterior sides; no sculpture. Tibia with one subapical baso-external spinule on anterior side, apex with three pairs of spinules on anterior and posterior sides; no sculpture. Tarsus with one subapical very small seta and one large pore posterior to seta, with one pair of apico-external spinules, with pair of subequal claws, and without empodium between claws; no sculpture.

Second Instar Larvae. *Diagnostic combination*.- As for first instar larva except: numerous accessory setae over most sclerites in addition to basic setae and pores, smaller pores with barely visible microsetae (referred to as accessory pores); egg-bursters absent from frontale; sculpture on parietal sclerite indistinctly expressed; apical cutting edge of mandible and/or posterior cutting edge of retinaculum not toothed, suggested or clearly toothed. Mesonotum, metanotum and terga 1 to 9 with anterior transverse bead; on terga 1 to 8 anterior bead extended laterally; mesonotal and metanotal epipleuron sharply defined from disc, posterior band of nota and terga diffusely defined from disc; irregular longitudinal channels on anterior bands of pronotum and prosternum, and on posterior bands of nota and terga; urogomphus with seven or more accessory setae, setigerous knobs nine or more , knobs prominent (though less than in third instar larva) or not so in one member; brown patterned surface well-outlined on nota and terga, alveolae isodiametric and relatively wider, each mesh with numerous micropores, alveolae outside brown patterned surfaces without micropores. Membrane sculpture more expanded than in first instar larva of most members; sculpture distribution slightly or not different among members.

Second Instar Larvae. Description.- Larger for each member: linear measurements on average about 1.5 times longer than their respective first instar larva. Coloration similar to first instar larva except in some members (described under each).

Head. Nasale lateral teeth present; frontal setae EMP and/or Mp absent (pore-like) or very small; frontale with three to eight accessory setae and pores, accessory setae very small to small; microsculpture lines absent or present in spots, alveolae absent or present antero-medially. Parietal sclerite dorsally without or with accessory small setae between DMM-P and DI-A, accessory pores present, number of accessory pores and/or setae seven to 10 or zero to five; laterally, surface delimited by setae DEP, VEP-P and VEM-P with three to nine accessory setae, seta VMA similar in size among members; sculpture less-expanded in many members, difference in sculpture between first and second instar minimal, slight, or in some members major, dorsal surface with pointed sculpture increased in most members up to 70%, or in others without points, ventral surface sculpture more lateral, and points absent or in some members up to 5% of surface, ventral surface with two fields of isodiametric or slightly transverse alveolae, one internal and one external to system VMM and VMP, in most members both fields connected posterior to system VMP.

Thorax. Pronotum with anterior and lateral bands sharply separated from disc and thinly sclerotized, posterior band not sharply separated from disc; anterior and posterior bands with irregular longitudinal channels; anterior, posterior and pronotal epipleuron with vermiculate black pigment; brown patterned surface similar in distribution and outline among members. Disc of pronotum with 15 to 95 accessory setae and zero to 30 accessory pores on each side of medial sulcus; posterior row of setae behind posterior row of basic setae small to large; microsculpture lines present or absent from disc and pronotal epipleruon, absent from anterior and posterior bands; alveolae of disc absent or present on up to 30% of surface, pointed sculpture absent or in some members expanded over 1% of surface; alveolae in brown patterned surface isodiametric, and relatively larger and with numerous micropores (visible under SEM); pronotal epipleuron without sculpture or small and single-pointed. Proepisternum with five to seven accessory setae; accessory setae small to medium; microsculpture lines absent or present, sculpture absent or single-pointed; surface without or with vermiculate black pigment. Proepimeron with one to seven accessory setae and zero to four pores; microsculpture lines absent or present, sculpture absent or single-pointed and/or multi-pointed. Prosternum posterior margin beaded; prosternum with two to 15 accessory setae; major pair of accessory setae small to large; no sculpture; black vermiculate pigment on anterior and postero-lateral bands.

Mesonotum with anterior band sharply separated from disc by transverse bead extended to antero-lateral corners, mesonotal epipleuron sharply separated and posterior band not sharply separated from disc; posterior band with irregular longitudinal channels; posterior band and mesonotal epipleuron with vermiculate black pigment; brown patterned surface as for pronotum but more complex; each side of mesonotum with eight to 70 accessory setae and nine to 12 accessory pores; major accessory setae on row behind posterior row of basic setae small to medium; microsculpture lines absent or present, alveolae absent or present up to 100% of surface on disc, pointed sculpture absent or present on disc, near suture up to 40% and laterally up to 60% of surface; pointed sculpture on anterior band up to 100% of surface and mesonotal epipleuron without sculpture or up to 100% of surface; alveolae of brown patterned surface as for pronotum. Mesepipleuron seta EP larger than first instar larva, small to large; mesepipleuron with one to 16 accessory setae and zero to seven accessory pores; size of major accessory setae very small to small; microsculpture lines absent or present, sculpture single-pointed and/or multi-pointed. Mesepisternum with one to six setae and no pores; microsculpture lines absent or present, sculpture single-pointed and/or multi-pointed. Mesepimeron with one to 10 accessory setae and zero to three pores; microsculpture lines absent or present, sculpture single-pointed and/or multi-pointed. Basic seta on anterior pleurite (AP) very small to medium. Mesosternite basic seta medium to large; mesosternite with zero to 10 accessory setae; accessory setae small to medium; no sculpture. Anterior sternite basic seta small to medium-large; anterior sternite with one to three accessory setae; accessory setae very small to small; no sculpture. Metathorax as above except pointed sculpture slightly more expanded and accessory setae slightly more numerous in most members.

Membrane microsculpture lines absent, sculpture expanded over most of surface; sculpture single-pointed, points virtually absent or well-defined.

Abdomen. Terga 1 to 8 with anterior and lateral bands sharply separated from disc, posterior band without or with irregular longitudinal channels; posterior band with vermiculate black pigment; urogomphus on tergum 9 without or with up to 50 (in most members nine to 12) raised setigerous punctures on knobs (especially puncture MAP-P); knobs absent from internal margin or present, knobs smaller than in third instar larva of the same species (Fig. 93b, 96a, 98b, 99a, 100a, 101a, and 103a); outline of brown patterned surfaces simpler than in mesonotum; setae AII and AIM of terga 2 to 8 small to medium, seta PII-P very small to medium-small, seta MPP-E on tergum 9 very small or small, and seta AM-P on tergum 10 small to very large; terga 1 to 7 with seven to 40 accessory setae on each side of tergum, tergum 8 with zero to 12 less setae than on preceeding terga, tergum 9 with seven to 30 accessory setae on urogomphus, tergum 10 with zero to three large major and zero to 22 minor accessory setae; size of major baso-lateral accessory setae in front of anterior row of basic setae small to medium, minor accessory setae on urogomphus extremely small or small, posterior major accessory seta on urogomphus relative to discal major accessory seta subequal or unequal; position of major baso-lateral seta or urogomphus lateral or more posteriorly baso-medially; microsculpture lines absent or present, sculpture on terga 1 to 8 single pointed or multi-pointed, points scattered or dense; sculpture on tergal surface on any of terga 1, 2, 3, 4, 6 or all terga; sculpture on urogomphus absent, suggested, or with scattered and fine single-pointed sculpture, or with dense and large single-pointed sculpture, or isodiametric alveolae, tergum with single-pointed and/or multi-pointed sculpture, anterior band on terga 1 to 9 without or with pointed sculpture over 10 to 100% of band surface; posterior band of terga 1 to 8 without or with sculpture over 5%, 10% or 100% of surface, alveolae of brown patterned surfaces as for pronotum. Abdominal epipleuron on segments 1 to 8 with eight to 30 accessory setae; no sculpture. Abdominal hypopleuron on segments 2 to 8 with four to 16 accessory setae (much less on segment 1); size of major accessory setae medium-small to very large, and size of minor setae small to medium-small; no sculpture. Abdominal sternite 1 with two to 16 accessory setae, segments 2 to 7 with 10 to 40, segment 8 with 10 to 50, segments 9 with zero to 26 accessory setae, and segment 10 with two to five major and zero to 22 minor accessory setae; average size of accessory setae on segments 2 to 7 mostly small to medium-small; microsculpture lines absent, sculpture on segments 2 to 9 single-pointed and/or multi-pointed. Internal abdominal postventrite (PsI) on segments 1 to 8 with accessory setae one to six, or absent; sculpture as on PsE but more restricted. Membrane microsculpture without lines, sculpture without or with extremely fine to coarse points; dorsal sculpture very narrowly to widely expanded over baso-lateral surface, lateral sculpture expanded over most of surface or more restricted, and ventral sculpture restricted baso-laterally or expanded over most of surface.

Third Instar Larvae. Diagnostic combination.- As in second instar larvae except: more accessory setae and pores on most sclerites, and setigerous knobs on urogomphus in lateral view, when present, larger than knobs of same members in second instar.

Third Instar Larvae. Description.- Larger than second instar larva of each member, linear measurements about 1.5 times longer than second instar larva. Coloration generally as for first instar larva, patterns on urogomphus in many members different and more clearly outlined than preceeding instars, or different (described for each member).

Head. Frontale with six to eight accessory setae; frontale with seta EA-A size very small to small, and with seta MP virtually absent or very small. Parietal sclerite with seta VMP-A size small to medium; alveolae ventro-laterally present to expanded laterally, sculptured fields external and internal to systems VMM and VMP more weakly impressed than in second instar. Prementum without or with one to 17 dorso-lateral accessory setae and ventrally with one to three accessory setae anterior to lateral basic seta.

Thorax. Brown patterned surface more clearly outlined, otherwise as for second instar larva. Disc of pronotum with 15 to 130 accessory setae and 30 to 80 accessory pores, pronotal epipleuron with two to 40 accessory setae and zero to 30 accessory pores; sculpture absent from disc or extended over surface, pointed sculpture absent or over 1% of surface; brown patterned surface as in second instar larva. Proepisternum with seven to 25 accessory setae; size of major accessory setae very small to medium-large. Proepimeron with one to 13 accessory setae and zero to 25 accessory pores. Prosternum with four to 15 accessory setae.

Disc of mesonotum with 20 to 110 accessory setae and 15 to 40 accessory pores on each half; posterior band laterally without or with one to 15 accessory setae; mesonotal epipleuron with one to 35 accessory setae and without or with one to 11 accessory pores; size of major accessory setae posterior to row of basic setae small to large; sculpture present over 20 to 100% of disc, pointed sculpture near suture absent or present up to 10% of disc surface, and laterally absent or present up to 15% of disc surface, pointed sculpture on anterior band absent or present up to 100% of band surface. Mesepipleuron with one to 40 accessory setae and with 10 to 25 accessory pores. Anterior pleurite of mesothorax with one to 11 accessory setae and without or with one to seven accessory pores; size of basic seta virtually absent to medium. Mesepimeron with one to 15 accessory setae and three to 20 accessory pores; size of basic seta very small to medium. Mesosternite without or with one to 10 small accessory setae. Metathorax as mesothorax except: accessory setae and pores slightly more numerous and pointed sculpture slightly more expanded.

Abdomen. Tergal epipleuron width on terga 1 to 8 average or very expanded; knobs of urogomphus in lateral view (Fig. 94, 96b, 97, 98c, 99b, 100b, 101b, 102 and 103b) indistinct to large and in dorsal view knobs virtually absent to large; disc of terga 1 to 7 with 15 to 100 accessory setae and on tergum 8 with zero to 20 less accessory setae than on preceeding terga, lateral band of terga 1 to 8 with five to 50 accessory setae, urogomphus with seven to 30 accessory setae, tergum 10 with zero to four major accessory setae and one to 22 smaller accessory setae; seta PII-P on terga 1 to 8 virtually absent to small, seta PI-P on tergum 10 small to large, and seta AM-P on tergum 10 small to very large; sculpture restricted on disc on any of terga 1 to 4, or on all terga. Abdominal epipleuron on segments 2 to 8 with eight to 60 accessory setae, on segment 1 with much fewer setae. Abdominal hypopleuron on segments 1 to 8 with eight to 50 accessory setae; size of major accessory setae on segments 1 to 8 medium-small to very large; sculpture on terga 2 to 4 without or with alveolae, sculpture absent to well developed. Abdominal sternite on segment 1 with two to 55 accessory setae, on segments 2 to 7 with 12 to 150, on segment 8 with 14 to 130, on segment 9 without or with one to 55, and on segment 10 with two to six major and zero to

24 minor accessory setae; average size of accessory setae on segments 2 to 7 small to medium; sculpture on segments 2 to 7 without or with lines, alveolae absent or present, sculpture single-pointed or multi-pointed, and points very fine to well-developed. External postventrite on segment 1 with 3 to 45 accessory setae and on segments 2 to 7 with four to 55. Internal postventrite on segment 1 with one to 23 accessory setae and on segments 2 to 7 with one to 26.

Membrane sculpture dorsally and ventrally on abdomen virtually absent or present baso-laterally to widely expanded.

Distribution.- The members of this tribe are found in all regions of the northern hemisphere (except for Greenland and Iceland) from the southern edge of the tundra to the southern half of the temperate zone (Morroco, southern California, northernmost Florida). Very few members are found in subhumid regions and none are found in desert areas.

3.2 Notes about Keys

The keys are intended for identification of specimens of extant articulate specimens, easily characterized by few structural characteristics. Fossils, however, come as fragments and require large amounts of information (students of fossils are referred to Diagnostic combination, Description). Larvae can be identified at species level if mounted in glycerine (see section 2.2.1). Probably in any one region larvae can be identified without such preparation, as the number of potential species is limited. I provide three keys: one to genera, one to subgenera of Elaphrus and one to species of these subgenera. Lindroth (1954) provided means for identification of known adults and larvae of species of Diacheila and Blethisa.

3.2.1 Key to Genera of Elaphrini

Adult stage

1. Pronotum with two pairs of setae near lateral margin. Elytron with well developed striae on disc (Fig. 28, 29, and 30); setigerous punctures absent from interval 7. Middle coxa with one or two setae. Head prognathous (Fig. 14 and 15). Frons elevated, dorsal margin of eye lower. Eyes small or normally developed. 2

1'. Pronotum without or with one pair of setae near hind angle. Elytral striae barely suggested near base or absent (Fig. 110 to 117) discal setigerous punctures on intervals 3, 5 and 7. Middle coxa with numerous setae. Head subhypognathous (Fig. 16). Frons concave between eyes, dorsal margin of eye higher; eyes very prominent. ....Elaphrus Fabricius p.106

2.(1). Pronotum margin narrow not explanate. Interval 3 of elytron without catenations (Fig. 28); setigerous punctures of disc on interval 3 only. Fronto-ocular sulcus indistinct (Fig. 14), punctures on most of surface of head. Clypeus without sublateral impression, thus surface smooth. Mentum with two setae (Fig. 8). ....*Diacheila* Motschulsky p.77

2'. Pronotum lateral margins very explanate. Elytral interval 3 and 5 with catenations (Fig. 29 and 30), setigerous punctures on disc present in interval 3 and 5; fronto-ocular sulcus deeply impressed and octagonal (Fig. 15); punctures absent from frons (absent or present posterior to eyes). Clypeus with sublateral impressions, thus surface embossed. Mentum with four setae (Fig. 9). ....*Blethisa* Bonelli p.86

Larval Stage

1. Nasale slightly projected (Fig. 87a), with teeth fine. Lacinia well developed with small or extremely small apical seta (Fig. 83 and 84). ....*Diacheila* Motchulsky p.77

1'. Nasale projected: medial projection much in front of adnasale projections (Fig. 88b to 92b), teeth on nasale fine, small or large. Lacinia cone-shaped with extremely small subapical seta (Fig. 83), and teeth of nasale large (Fig. 88b), or lacinia suggested, with small seta, and teeth of nasale absent, fine or small (Fig. 89b to 92b). 2

2. (1'). Teeth of nasale very large (Fig. 88b), meeting at middle. Base of mandible narrow, baso-internal margin apparently continuous with apico-internal margin (Fig. 78) Lacinia well developed; subapical seta extremely small (Fig. 83).
.... Blethisa Bonelli p.86

2' Teeth of nasale absent, fine, small, or large and separated by toothless medial projection (Fig. 89b to 92b). Base of mandible wider, thus internal margin not apparently continuous with apico-internal margin (Fig. 80 and 81). Lacinia absent or suggested; apical seta small.
.... Elaphrus Fabricius p.106

3.2.2 Recognition of Sex in Adults and Larval Instar Stages

Males of Carabidae are generally recognized by enlarged basal tarsomeres of forelegs, and by presence of white hair-like structures ventrally, termed spongy pubescence in elaphrine beetles. Elaphrines show spongy pubescence under tarsomeres 1 to 3 or 1 to 4 except in members of E. punctatus Motschulsky where sexes are recognized by their genitalia only. In many members males have a small tooth-like projection on the internal apical angle of the tibia of midleg, in some members males are more densely setose medially on abdominal sterna especially on sternum 7, in few members males show tooth-like projections at base of apical spur and of posterior spur of tibia of foreleg, or only at base of posterior spur, or, in one member, males present a very large projection beneath femur of foreleg.

Recognition of first larval instar is easy but separation of second and third instar larvae is difficult since I failed to find one single common character except that accessory setae on most sclerites are increased for each member species. Recognition of these instar larvae can only be done after determination of the genus and subgenus. Fortunately genera and subgenera are recognized by many structural characters common to all instar larvae of each taxon. The following key provides the necessary information. In couplet 2 locate the description of the genus or subgenus of your specimen then compare couplet 2 and 2' for this genus or subgenus. Characteristics in couplet 2 describe second instar larvae, and those of couplet 2' the third instar larvae.

Key for recognition of larval instars

1. Egg-bursters parallel black keels laterally on frontale (Fig. 87). Meshes of microsculpture absent ventrally from parietale both sides of

systems VMM and VMP. Numbers of basic setae and pores on sclerites as illustrated (Fig. 76)--terga 1 to 8 each with two rows of three setae, and urogomphus of tergum with five basic setae. ....First instar larva

1'. Egg-bursters absent from frontale. Field of meshes of microsculpture ventrally on parietale on both sides of systems VMM and VMP. In addition to basic setae and pores of first instar, many accessory setae and microsetae (new added pores seem to bear microsetae) and urogomphus of tergum 9 in addition with seven to 30 accessory major setae (Fig. 93b, 94, 96, 98b, 99, 100, 101, and 103). 2

2.(1'). Diacheila. Knobs of urogomphus of tergum 9 0.5 as small as those of third instar larvae (Fig. 93b and 94).

Blethisa. Pronotal epipleuron with 20 or less accessory setae, mesonotal disc with 70 or less, mesonotal epipleuron with 15 or less, sternite of segments 2 to 7 with 40 or less, and external poststernite on segments 2 to 7 with 10 or less.

Elaphrus (Arctelaphrus). Head width 0.8 mm. (I have not seen the second instar larvae, but number of accessory setae follows a pattern similar to members of subgenus Elaphrus, thus I assume the following would apply). Mesonotal and metanotal disc with 10 or less accessory setae, abdominal epipleuron of segments 2 to 8 with 10 or less, abdominal segment 9 without, and external poststernite of segments 2 to 7 with 5 or less.

Elaphrus (Neoelaphrus). Proepisternum with five or less accessory setae, disc of mesonotum and metanotum with 15 or less, external poststernite of segments 2 to 7 with seven or less.

Elaphrus (Elaphrus). Disc of pronotum with 15 or less accessory setae, disc of mesonotum and metanotum with 10 or less, disc of terga 1 to 8 with 9 or less, hypopleuron of segments 2 to 8 with four or less, and sternite of segments 2 to 8 with 10 or less. Urogomphus of tergum 9 with knobs 0.5 as small as third instar larvae (Fig. 100).

Elaphrus (Elaphroterus). Proepisternum with seven or less accessory setae, disc of terga 1 to 8 with 30 or less, hypopleuron of segments 2 to 8 with eight or less, sternite of segments 2 to 8 with 14 or less, and external poststernite of segments 2 to 7 with four or less.

..........................Second instar larvae

2'. Diacheila. Urogomphus knobs of tergum 9 large (Fig. 94).

Blethisa. Pronotal epipleuron with 30 or more accessory setae, disc of mesonotum with 90 or more, mesonotal epipleuron with 20 or more, sternite of segments 2 to 7 with 90 or more, and external poststernite or segments 1 to 7 with 30 or more.

Elaphrus (Arctelaphrus). Head width 1.1 mm. Disc of mesonotum and metanotum with 16 accessory setae, epipleuron of segments 2 to 8 with 18, hypopleuron of segments 1 to 8 with 19, sternite of segment 9 with eight, and external poststernite on segments 2 to 7 with seven.

Elaphrus (Neoelaphrus). Proepisternum with 25 or more accessory setae, disc of mesonotum and metanotum with 25 or more, and external poststernite of segments 2 to 7 with 9 or more.

Elaphrus (Elaphrus). Disc of pronotum, mesonotum and metanotum with 21 or more accessory setae, terga 1 to 8 with 17 or more, hypopleuron of segments 2 to 8 with eight or more, sternites of segments 2 to 8 with 14 or more. Urogomphus knobs of tergum 9 large (Fig. 100).

Elaphrus (Elaphroterus). Proepisternum with 10 or more accessory setae, disc of terga 1 to 8 with 40 or more, hypopleuron of segments 2 to 8 with 12 or more, sternite of segments 2 to 8 with 28 or more, and external poststernite of segments 2 to 7 with seven or more ....Third instar larva

3.3 Genus *Diacheila* Motschulsky

Diacheila Motschulsky 1845: 75. *Type species*.- *Diacheila arctica* Gyllenhal 1810: 96 (subsequent designation by Lindroth, 1961: 102). Lindroth 1954: 4.

Diachila auctorum. Invalid emendation of first original spelling, by Motschulsky(1850). Anonymous 1928-1954.

Diaheila Motschulsky 1845: 75. Different spelling of this genus by Motschulsky but not appearing first in text (Lindroth, 1961).

Arctobia Thomson 1859: 194. *Type species*.- *Diacheila arctica* Gyllenhal 1810: 96. Lindroth, 1961.

Adults. *Diagnostic combination*.- Anterior fringe of prosternum medially with long narrow setae and laterally with small scimitar-shaped setae; metasternum with numerous punctures at least laterally and without setae; stridulatory scraper plate on tergum 7 with few points (11) and closer (20 microns) to each other; abdominal sterna 2 and 3 with numerous punctures and sterna without other setae than ambulatory setae, abdominal sternum 7 with two setae on posterior margin; elytral striae average for carabids, striae straight or sinuate near discal setigerous punctures thus intervale not catenate; elytral epipleuron with few punctures distributed along weakly defined sulci; median lobe of males with small narrow stylet; median lobe base and ventral surface not distinctly more sclerotized than lateral surfaces (Fig. 38); females basal sclerite of stylus with fine spinules on dorso-lateral ridges (Fig. 70); protibial rows of setae shorter than tibia; posterior internal row of mesotibia with few (five to six) setae; hind coxa with one large discal seta and two interno-subapical medium setae; hind femur with three to five setae.

Adults. Description.- Medium-large beetles 7.0 to 9.0 mm. Body moderately narrow. Upper surface dark green or copper, or dark piceous with metallic reflections, ventral surface and appendages black and/or piceous. Pores in punctures small or, in members of D. polita large. Integument shiny or dull, microsculpture mostly absent or well developed on sclerites.

Head. Head capsule (Fig. 14) with punctures dorsally and laterally near eyes; fronto-ocular sulcus very shallowly impressed; eyes average or small; microsculpture lines absent or present, alveolae flat. Clypeus with punctures or with micropunctures; one seta medio-sublaterally; surface smooth; microsculpture lines absent or present, alveolae flat. Labrum sculpture with flat or convex alveolae.

Antenna. Antennomere 3 with flat pubescence except for few apical setae; antennomere 2 0.4 length of antennomere 3.

Mouthparts. Left mandible with molar, basal retinacular and terebral tooth small, and apical retinacular tooth absent; right mandible with small and single basal retinacular tooth and small terebral tooth (Fig. 2). Lacinia spinules on internal margin alternatively small and smaller;

larger spinules and apical projection of lacinia subequal in length to width of lacinia. Stipes ventral surface with microsculpture lines medially, alveolae flat or indistinct. Maxillary palpomere (Fig. 5) 3 0.5 length of palpomere 4, palpomere 2 1.5 length of palpomere 3; microsculpture lines present, alveolae flat. Galeomere 1 1.5 length of galeomere 2, galeomere 2 0.75 length of maxillary palpomere 4. Anterior transverse expansion of submentum with eight setae; microsculpture lines absent from most of surface except at base or absent behind transverse expansion, alveolae flat or convex at base. Mentum with two medial setae. Labial palpomere 2 0.67 length of palpomere 3. Length of mentum medial teeth 0.5 depth of mentum emargination, emargination of medial tooth 0.3 to 0.5 teeth length (Fig. 8). Ligula projected.

Thorax. Pronotum side not broadly reflexed; lateral bead narrow or wide; lateral bead extended from anterior to posterior lateral angles; postero-lateral impression without or with carina; surface without discal impressions; fringe of setae on anterior and posterior margins not reaching lateral angles; setae of fringe scimitar-shaped, setae at middle 0.67 length of lateral ones; pronotum lateral margin with two setae; punctures present and uniformly distributed; punctures 20 microns in size, 50 microns apart, puncture edge sharply outlined on 30% of circumference; sculpture absent or lines present, alveolae flat or convex; Proepisternum with incomplete sulcus between internal flange and external episternum at junction with pronotum epipleuron; flange small; punctures 15 microns in size, 45 to 75 microns apart, and edge of punctures sharply outlined on 30% of circumference; microsculpture lines present or absent, alveolae flat. Proepimeron punctures 25 microns in size, 25 to 100 microns apart, edge of punctures sharply outlined on 30% of circumference; sculpture as on proepisternum. Prosternal suture slightly sinuate not suddenly constricted; fringe on anterior margin with long narrow setae medially and smaller scimitar-shaped setae laterally; punctures 20 microns in size, 60 to 100 microns apart, and edge of puncture sharply outlined on 60% of circumference; no setae on surface; sculpture absent or lines present, alveolae flat. Scutellum of mesothorax without transverse sulcus near base (subapically near level of basal stria with one or two indistinct sulci); lateral ridge complete; puncture present at base; pores in punctures small; microsculpture lines present at base and absent apically, alveolae flat or convex. Mesepisternum anterior discal ridge indistinct or well defined; punctures 25 microns in size, 25 to 50 microns apart; sculpture absent or lines present laterally, alveolae flat. Mesepimeron punctures 25 microns in size, 25 to 50 microns apart; sculpture absent or lines present and indistinctly impressed. Mesosternum without postero-lateral transverse ridge; punctures present laterally, punctures 25 microns in size, 25 to 75 microns apart; setae absent from surface;

microsculpture lines present at base, lines of alveolae weakly defined or flat.

Metanotum with very small apico-submedial setae; metanotum with few discal setae. Metepisternum with indistinctly or well outlined anterior ridge; punctures 30 microns in size, 30 to 90 microns apart, and edge of punctures sharply outlined on 50% of circumference; sculpture absent or lines present, alveolae flat. Punctures of metasternum 25 microns in size, 50 to 100 microns apart, edge of puncture sharply outlined on 50% of circumference; setae absent from surface; anterior process with complete or laterally restricted ridge; microsculpture lines absent or present, alveolae flat.

Abdomen. Tergum 2 with medio-basal ridge on each side of mid-line; tergum 7 with 11 points on stridulatory scraper, points 20 microns apart; setae absent from tergum 1; discal sculpture of tergum 8 with lines, alveolae flat. posterior margin of sternum 7 with two apical setae; punctures on sternum 2 and at least laterally on sternum 3, and sternum 4 without or with lateral punctures, punctures 25 microns in size, 10 to 100 microns apart, edge of puncture sharply outlined on 50% of circumference; no setae on surface except for ambulatory setae; microsculpture lines absent or present, alveolae flat.

Elytra. Most striae clearly defined at least medially; base of stria 5 indistinctly or deeply impressed; basal transverse stria extended to stria 5 or terminated at humerus striae straight or slightly sinuate near setigerous punctures; intervale not catenate, but slightly or not impressed near setigerous punctures (Fig. 28); interval 3 with four to seven setigerous punctures, interval 9 with six or 10 umbilicate punctures, all setigerous punctures small; punctures near setigerous punctures absent; striae punctate, punctures 25 microns in size, 25 to 200 microns apart; pores in punctures small; microsculpture lines absent or present in spots, alveolae flat to convex on entire surface, alveolae on elytra or restricted to posterior 0.33. Elytral epipleuron with punctures along indistinctly outlined sulci, punctures 30 to 40 microns in size, 35 to 70 microns apart.

Wings. Very similar to those of members of Blethisa with oblongum posterior end rounded (Fig. 33).

Legs. Coxa of foreleg without setae; punctures present, 25 microns in size, 50 to 200 microns apart, edge of puncture sharply outlined on 30% of circumference, Trochanter with two setae; sculpture as on coxa. Femur without internal medial projection; setae 20 or less; sculpture absent or lines present, alveolae flat. Tibia without internal projections at base of apical and posterior spurs; fringe (anterior internal row) 0.4 to 0.5 length of tibia; setae of posterior medial row not expanded near apex; posterior medial row with seven setae on 0.5 of tibia, posterior internal row with six setae along tibia length, row posterior to fringe with four setae extended toward base of tibia; sculpture on tibia absent or lines present, alveolae convex. Tarsomeres 1 to 4 enlarged and with spongy pubescence ventrally; tarsomeres 1 to 4 with five to six ventral spinules and tarsomere 5 with four spinules; sculpture as on tibia.

Coxa of midleg without or with punctures, punctures 25 microns in size, 25 to 100 microns apart, edge of punctures sharply outlined on 50% of circumference; coxa with two setae; sculpture lines present, alveolae flat. Trochanter with one seta; sculpture as on coxa. Femur internal surface without angular projection; femur with 20 or less setae; sculpture absent or lines present, alveolae flat. Tibia without internal apical projection in males; anterior internal row with few setae (five to six); setae of anterior medial and internal, and posterior internal rows not expanded near apex; sculpture as on femur. Tarsomeres 1 to 4 with four to eight ventral spinules, and tarsomere 5 with eight ventral spinules.

Coxa of hind leg without or with punctures, punctures 25 microns in size, 25 microns apart, edge of punctures sharply outlined on 50% of circumference; coxa with three setae: one large discal and two interno-subapical setae; sculpture lines present, alveolae flat. Trochanter posterior surface with five or six spinules; sculpture as on coxa. Femur with three to five setae; sculpture lines absent or present, alveolae flat. Tibia without external row of setae; setae of anterior medial and internal, posterior internal rows not expanded near apex; sculpture lines absent or present in spots, meshes present at least apically, alveolae flat or convex. Tarsomeres 1 to 4 with eight spinules, and tarsomere 5 with six spinules; sculpture lines present, alveolae flat or convex.

Male genitalia. Basal and ventral surfaces not more distinctly sclerotized than lateral surfaces, dorsum of lobe sclerotized near base, membranous in apical 0.5. Stylet shorter than in members of other genera and very slender (Fig. 38).

Ovipositor. Female basal sclerite of style with dorsolateral ridges, ridge with few spinules, spinules present apico- ventrally; apical sclerite with few fine spinules, apex with two small setae (Fig. 70).

Taxonomic notes.- Lindroth (1954) recognized three extant species. I had the opportunity to study in detail two: Diacheila arctica Gyllenhal and D. polita Faldermann, and briefly I looked at D. fausti Heyden. I will not discuss Lindroth's species further as the review is most satisfactory.

Third Instar Larvae. Diagnostic combination.- Nasale little projected, nasale level with or projected beyond adnasale (Fig. 87b) Apical cutting edge of mandible without or with well developed fine teeth (Fig. 78 and 79); retinaculum not toothed; retinaculum typical or twice as long. Stipes with well developed conical lacinia (Fig. 83c and 84); seta of lacinia apical and slightly smaller than seta on stipes internal margin near lacinia, or subapical and very small. Terga with two rows of four setae, other accessory setae apparently absent.

Third Instar Larvae. Description.- Head. Frontale with nasale little projected medially, nasale projection level with or beyond adnasale projection; teeth on nasale fine and numerous, teeth extended to middle or not. Base of mandible narrow: posterior internal margin seemingly continuous with anterior cutting edge; anterior cutting edge without or with fine teeth, retinaculum without teeth on posterior margin, retinaculum typical or twice as long. Lacinia conical; seta apical and, slightly smaller than seta just behind lacinia along stipes internal margin or seta subapical and very small. Anterior seta on external margin of stipes posterior to level of lacinia. Ligula prominent.

Abdomen. Terga 1 to 8 with two rows of four setae, other accessory setae apparently absent. Urogomphus of tergum 9 with very prominent knobs in dorsal and lateral views, but without knobs along internal margin; urogomphus with about seven accessory setae; seta MPP-E size on tergum 9 small.

Taxonomic notes.- This peculiar larva was described by Lindroth (1954). I have no doubt about its identity. I failed to relocate the original specimen, thus this description is based on Lindroth's description and key characters.

Distribution.- Members of this genus are found from subarctic and arctic Scandinavia to Labrador, and are found in mountains of Siberia with one relict member along the Tien-Shan mountains in Western China and neighbouring USSR (Lindroth, 1954). I have seen a few representatives of the three known species of adults. I know the third instar larva of *D. arctica* from description only (Lindroth, 1954) but I examined six first instar and three second instar larvae of *D. polita* from the Anderson River delta, Northwest Territories.

3.4 Genus *Blethisa* Bonelli

Blethisa Bonelli 1810. *Type species*.- *Blethisa multipunctata* Linnaeus 1758: 416. Lindroth 1954: 10.

Helobium Leach 1815. *Type species*.- *Helobium multipunctatum* Linnaeus 1758: 416.

Rhaphiona Fischer 1829. *Type species*.- *Rhaphiona eschscholtzi* Zoubkoff 1829: 155.

Adults. *Diagnostic combination*.- Fronto-ocular sulcus very well impressed, shaped as 8 (Fig. 15); upper ring of ocular sulcus with both supra-ocular setigerous punctures; punctures on head capsule absent or restricted to posterior portion. Clypeus surface with weak sublateral impressions, thus embossed between; no punctures. Labrum sculpture lines absent or present laterally, alveolae indistinctly outlined. Left mandible with apical retinacular tooth level with terebral tooth. Maxillary palpomere 3 0.67 length of palpomere 4. Mentum with four setae: two sublateral and two submedial setae; labial palpomere 1 0.5 length of palpomere 2 and 0.8 length of maxillary palpomere 4. Pronotum margin very explanate; setae of fringe of anterior and posterior margins narrow. Prosternum anterior margin with fringe, fringe formed of narrow setae. Proepisternum with complete suture at junction of external disc with internal flange. Scutellum with basal transverse sulcus (posterior to weak transverse impressions at level of basal transverse stria); lateral sulcus not complete to apex. Mesosternum with postero-lateral ridge. Metanotum with large postero-lateral ridge. Metanotum with large apico-lateral setae. Metasternum without or with very few lateral punctures, punctures not sharply defined; no setae on surface except in one member with dense postero-medial brush. Tergum 1 with numerous setae, setae absent from midline; tergum 8 sculpture absent apically. Abdominal sterna without punctures, or with few indistinctly defined punctures laterally on sternum 1. Striae 1 to 6 clearly defined, remaining stria suggested, or very irregular and in some members catenate or absent; intervals 3 and 5 catenate (irregular catenations present in some members in area of seventh interval), catenation completed behind setigerous punctures (Fig. 30), catenation not forming mirrors though in some members brighter; discal setigerous punctures on interval 3 and 5; no punctures on elytral epipleuron. Coxa of foreleg without punctures.

Trochanter of foreleg with one seta. Trochanter of midleg without seta. Coxa of hind leg with two setae: one large discal and one interno-subapical seta (in one member with internal brush of setae). Trochanter of hind leg with many posterior spinules (10 to 15). Femur of hind leg with one seta. Basal sclerite of stylus of female with numerous setae in apical 0.67 (Fig. 71); apical sclerite with numerous small spinules; dorso-apical ridge on basal sclerite absent.

Adults. Description.- Medium-large to large beetles: 10 to 18 mm. Pronotum wide. Upper surface black, or dark copper, or copper or green; ventral surface black or with dark metallic reflections. Sculpture lines on upper surface, alveolae flat to convex; pores in punctures small.

Head. Head outline average for carabids; eyes well developed; fronto-ocular sulcus deeply impressed and shaped as 8 (Fig. 15); posterior ring of ocular sulcus with both supra-ocular setigerous punctures; punctures on head capsule absent or restricted to portion of head behind eyes; sculpture lines present, alveolae weakly defined. Clypeus with sublateral impressions, thus surface embossed on each side of impression. Labrum sculpture without or with lines, meshes absent or restricted laterally.

Antennae. Antennomere 1 2.0 length of antennomere 2, antennomere 2 0.4 length of antennomere 3; sculpture lines present, alveolae flat, weakly or well defined.

Mouthparts. Grinding edge of right mandible 0.5 length of mandible; basal retinacular and terebral tooth small or large; apical retinacular tooth of left mandible level with terebral tooth (Fig. 1). Sculpture lines present on ventral surface of stipes, alveolae weakly defined. Lacinia spines on internal margin alternatively small and smaller, lacinia apical projection as long as or slightly longer than lacinia width, spines on internal margin of lacinia as long as lacinia width. Maxillary palpomere 1 (Fig. 6) 0.33 to 0.4 length of palpomere 2, palpomere 2 1.5 length of palpomere 3, palpomere 3 0.67 length of palpomere 4; sculpture lines present on maxillary palpus, alveolae weakly defined. Galeomere 1 2 times length of galeomere 2, galeomere 1 as long as maxillary palpomere 2, galeomere 2 0.8 length of maxillary palpomere 4. Anterior expansion of gula with 8 setae; sculpture lines present, alveolae flat and on base convex. Mentum (Fig. 9) with four setae: two sublateral and two submedial; length of mentum medial teeth 0.5 depth of mentum emargination, emargination between medial teeth 0.67 length of medial teeth; sculpture lines present, alveolae flat. Ligula prominent. Labial palpomere 2 0.5 length of palpomere 3.

Thorax. Pronotum with two setae along lateral margin; postero-lateral impressions without or with lateral carina; lateral margin very explanate; setae of fringe along anterior and posterior margin narrow; fringes well removed from lateral angles; punctures absent or present, weakly defined and denser laterally; sculpture lines present, alveolae flat. Proepisternum with complete sulcus between external disc and internal flange; punctures absent or present, puncture 25 microns in size, and shallowly impressed; sculpture with lines, alveolae flat. Proepimeron without or with punctures, punctures 25 microns in size, and shallowly impressed; sculpture as on episternum. Prosternum lateral suture slightly sinuate; setae of fringe on anterior margin as on pronotum; punctures absent or very scattered on disc and shallowly impressed; sculpture lines present, alveolae flat to convex, posteriorly alveolae isodiametric or anteriorly slightly transverse, sculpture in coxal cavity formed of small points.

Scutellum with transverse ridge basally and with lateral ridges ended before posterior apex; no punctures; sculpture lines present, alveolae flat and shallowly impressed; sculpture absent medio-posteriorly, alveolae flat, in some members, alveolae indistinct anteriorly. Mesepimeron without punctures; sculpture lines present, alveolae flat. Postero-lateral ridge of mesosternum well developed; punctures absent or laterally present, punctures shallowly impressed; setae absent.

Postero-lateral setae of metanotum medium in size; disc with numerous or few (about 10) setae. Anterior ridge of metepisternum well developed; punctures absent or present, punctures shallowly impressed; setae absent; sculpture lines present, alveolae flat to convex. Punctures on metasternum absent or with few scattered and indistinct setae; no setae except in one member with postero-medial brush of setae;

sculpture absent or present, alveolae flat, indistinct and, in part, slightly transverse on disc.

Abdomen. Stridulatory plates on tergum 7 with 20 to 25 points, points 30 microns apart; postero-medial ridges on tergum 2 absent; tergum 1 with numerous medium-small setae, setae absent from middle; tergum 7 without or with setae along anterior margin; tergum 8 with numerous setae; sculpture lines absent or present, alveolae flat restricted to disc. Abdominal sterna without or with punctures, punctures restricted to lateral portion of sternum 2 and very shallowly impressed; sternum 7 with two pairs of setae along posterior margin, sterna 2 to 6 without or with accessory setae between ambulatory setae, sternum 7 without accessory setae; sculpture lines present, alveolae indistinct on disc.

Elytra. Striae well defined up to sixth one, remaining one absent or weakly expressed, or irregularly interrupted; intervals 3 and 5 catenate, catenation completed behind setigerous punctures or before and after setigerous punctures (Fig. 29); stria 5 slightly impressed near base; transverse basal stria extended to scutellum or reaching stria 5; setigerous punctures on disc restricted to intervale 3 and 5, interval 3 with five to six, interval 5 with two to four, and interval 9 with nine to 10 setigerous punctures, setigerous punctures small; punctures restricted to striae on disc, puncture 25 to 45 microns in size, 90 to 130 microns apart, and shallowly impressed; sculpture lines present, alveolae flat on disc or convex laterally and subapically. Epipleuron without punctures. Stridulatory file well developed on ventral side on internal lateral ridge near apex.

Wings. Similar to those of members of Diacheila (Fig. 33) Oblongum posterior end rounded.

Legs. Coxa of foreleg without puncture or setae; sculpture lines present, alveolae flat. Trochanter with one seta; sculpture lines absent. Femur without or with large medial projection on internal side; surface with few (16 or less) setae; sculpture lines present. Meshes flat and weakly defined or well developed. Tibia without internal apical and/or internal medial projections; anterior medial fringe short (0.33 length of tibia), and with few setae posteriorly, posterior medial row with few setae (six) setae, and row short (0.5 length of tibia), and setae not expanded near apex, posterior internal row with few (three to four) setae; no sculpture. Tarsomeres 1 to 4 on internal side with spongy pubescence in males and with five to eight setae, and tarsomere 5 with five to six setae; no sculpture.

Coxa of midleg with one or two setae; no puncture; sculpture lines present, alveolae flat, alveolae, in part, slightly transverse. Trochanter without setae; sculpture lines present, alveolae flat and indistinct. Femur internal medial surface weakly protruding or smooth; surface with few (20 or less) setae; sculpture lines present, alveolae flat and indistinct or distinct. Tibia of males without or with apico-internal projection; surface with about 40 setae, anterior internal row with 10 setae or less, row of setae of anterior medial and internal, and posterior internal rows not expanded near apex; sculpture lines absent or, at least near apex present, alveolae flat. Tarsomeres 1 to 5 with five to six setae.

Coxa of hind leg without punctures; surface with two setae: one large discal and one medium interno-subapical seta, or in addition, in one member with an internal brush; sculpture lines present, alveolae flat. Trochanter with many (10 to 15) small spinules on posterior surface; sculpture as on coxa. Tibia without external row of setae; surface with about 40 setae, posterior internal row with few setae (nine or 10), anterior medial row with few (6) setae, and row short (0.5 length of tibia); row of setae of posterior internal, and anterior medial and internal rows not expanded near apex; sculpture as on coxa; Tarsomeres 1 to 4 with eight to 10 internal setae, and tarsomere 5 with six internal setae.

Male genitalia. Baso-lateral and ventral surface of median lobe with thickly sclerotized surface, lateral surface thinly sclerotized and sharply divided from the above (Fig. 39); basal orifice open dorsally; apex of lobe in lateral view spatulate or with large or very small ventral points. Stylet in lobe very large, protruded well beyond basal orifice; anterior end spatulate for muscle attachment. Lateral lobes very long about as long as median lobe; setae along posterior margin relatively short about 0.5 width of lobes.

Ovipositor. Tergum 9 and valvifer with scattered small setae. Basal sclerite of stylus with numerous setae in apical 0.67 (Fig. 71); no dorso-lateral ridge. Apical sclerite with many very small spinules on surface, apex with two small setae.

First Instar Larvae. *Diagnostic combination*.- Larvae body length large 7 mm (after hatching). Teeth on nasale very large (Fig. 88b); frontale seta EMP size small. Angle formed by seta DI-A, and pores DI-P and DMP-E very open (about 160°); position of pore VEP-A more internal relative to seta VEP-P, pore and seta of system VEM closer as pore VEM-A behind po posterior margin of eyes; setae DEP, VEP-P and VMP-A very large, seta VMA size large, and seta VEM-P size medium-large; sculpture lines present on parietale dorsal surface and restricted laterally on ventral surface. Width at eye level relatively wider: PW/PML 1.13 to 1.25, and width at base relatively narrower: PML/PBW 1.05 to 1.21. Antennomere 2 subequal to or 0.67 length of antennomere 3. Maxillary stipes long 3.5 to 5.0 times longer than wide; lacinia conical, subapical seta extremely small, seta behind lacinia on internal margin of stipes small about 10 times longer than seta of lacinia; galeomere 2 with extremely small lateral seta restricted to basal 0.5 to 0.33. Basic proepisternal and proepimeral seta size medium. Mesothoracic and metathoracic epipleural seta very large. Abdominal terga 1 to 8 with setae AII and AIM size large, and with seta PII-P medium-small, on tergum 10 seta AM-P size large; sculpture on terga 1 to 8 single-pointed anteriorly, and on urogomphus of tergum 9 with wide scales or crenulated wide scales. Abdominal epipleuron 9 with seta Ep-A size medium-small to large, size of Ep-A similar on segments 2 to 9. Internal poststernite on segments 1 to 8 with small to medium-small seta PsI-I. Membrane sculpture very restricted dorsally and laterally, on abdomen present near epipleuron and narrowly extended to postero-lateral angle of tergum.

First Instar Larvae. _Description_.- Size large 7 to 10 mm. Dorsally parietale pale laterally or basally, and on ventral surface parietale pale basally.

Head. Frontale projected well beyond adnasale level (Fig. 88a), teeth extended on nasale, teeth very large; seta MMP-E position internal to eggburster anterior end, pore MA-I in front of seta MMA; seta EMP size small, setae EA-E and MP size small to medium-small. Epicranial suture of parietale as long as first antennomere; head elongated, convexity of margin anterior to neck longer than convexity posterior to neck; seta DI-A position posterior to frontale postero-lateral angle, system DMM with DMM-P level with frontal postero-lateral angle, triangle formed by setae DEP, VEP-P and VEM-P elongated anteriorly, angle formed by seta DI-A and pores DI-P and DMP-E opened (about 160°), VEM-A posterior to hind margin of eye, thus closer to seta VEM-P, pore VEP-A external to seta VEP-P; setae DEP and VMP-A size large to very large, seta DMM-A size medium, seta DI-A size medium-large to large, setae DMP-A and VEM-P size medium-large, seta VMA size large, and seta VEP-P size very large; dorsal surface and ventrally along lateral margin with sculpture, sculpture on parietale without points.

Head proportions (Fig. 77) as follows: PLP/PlP 1.8 to 3.1, PlP/PlA 2.7 to 4.2, PW/PML 1.13 to 1.25, PW/PLP 1.6 to 1.8, PML/PBW 1.05 to 1.21, FW/OL 4.1 to 4.7, PL/OL 3.5 to 4.4, Fl/OL 3.0 to 4.0, Pl/OL 1.5 to 1.9, Pl/PL 4.0 to 4.6, and FW/PL 1.02 to 1.08.

Antennae. Antennomere 2 subequal to or 0.67 length of antennomere 3.

Mouthparts. Mandible postero-internal margin narrow: margin seemingly continuous with anterior cutting edge; retinaculum posterior margin and anterior cutting edge with very small teeth. Maxillary stipes elongate 3.5 to 5.0 times longer than wide; external margin behind posterior lateral seta sclerotized and not protruded outward; anterior seta along external margin of stipes anterior to lacinia level; ventral posterior pores as far apart as length of galeomere 1; setae on internal 0.5 of dorsal surface of stipes moderately dense (20 to 30), setae extended in anterior 0.33 roughly in one row; pointed sculpture on external dorsal 0.5 of stipes on most of stipes length. Lacinia prominent and cone-shaped; subapical lacinia seta extremely small, about 0.1 length of seta posterior to lacinia along stipes internal margin. Maxillary palpomere 1 1.5 length of palpomere 2. Position of microseta along internal margin of galeomere 2 in basal 0.33 to 0.5 length of galeomere 2; seta size of galeomere 1 very small to small. Ligula wide and prominent; dorso-lateral spinule size of prementum small.

Thorax. Pronotal seta AII-E size large to medium-large, setae MI, ME-I and PII-P medium-small to medium; sculpture present on 5 to 10% of pronotal disc, pointed sculpture present on 5% of disc or absent. Proepisternal and proepimeral seta size medium.

Mesonotal setae AIM and AIE-I size medium to large, setae PIM-I and PIE-A size large to very large, seta PII-P medium-small to medium; sculpture present on 20 to 40% of surface, pointed sculpture on 5 to 10% of surface near suture, on 5% laterally, and absent from posterior band. Epipleural seta size large. Size of anterior sternite (AS) seta size small to medium-small. Size of sternite seta medium. Metathorax as mesothorax. Membrane sculpture absent from dorsal surface, present on 50% of lateral surface, and on 30 to 50% of ventral surface.

Abdomen. Setae AII and AIM size on terga 1 to 8 large, seta PII-P size on terga 1 to 8 medium-small, seta AM-P size on tergum 10 large to very large; sculpture of terga 1 to 8 single-pointed or multi-pointed (one to three points associated), urogomphus of tergum 9 formed by scales or crenulated scales, and on tergum 10 sculpture single-pointed or multi-pointed. Size of epipleuron seta on tergum 1 medium-large, on terga 2 to 8 large, on tergum 9 as large or medium. Setae of sternite on segments 2 to 7 medium; sculpture on segments 2 to 7 absent, on segment 8 on 10%, on segment 9 on 25%, and on segment 10 on 100% of surface. External poststernite anterior seta (PsE)A size medium to medium-large. Internal poststernite interior seta (PsI)I size on segments 1 to 8 small to medium-small, and on segment 9 medium-small to medium.

Membrane sculpture dorsally restricted baso-laterally, extended laterally around epipleuron, and absent ventrally on segments 2 to 7 and expanded baso-laterally on segments 8 and 9.

Second Instar Larvae. Diagnostic combination.- Size large 9 to 15 mm. Frontale dorsal surface with three accessory setae on disc; accessory setae small; antero-discal field of sculpture present. Parietal with seven to eight accessory setae on lateral surface; sculpture lines ventrally on both sides of systems VMM and VMP present, alveolae convex. Stipes ventrally with three antero-discal, with few ventral postero-lateral and, in one member, dorsally with few postero-lateral accessory setae. Pronotum with 95 accessory setae on each 0.5, and with 12 to 14 accessory setae on pronotal epipleuron; size of largest accessory seta on pronotal epipleuron medium to large. Proepimeron with 5 to 7 accessory setae. Size of anterior pleurite (AP) major accessory setae medium. Prosternum with

10 accessory setae on posterior band medium. Mesonotum and metanotum on disc with 60 to 70 accessory setae on each 0.5, and on epipleuron and epipleuron of this nota with 7 to 13 accessory setae; size of epipleuron major accessory setae of these nota small to medium-small. Mesepisternum and metepisternum with three to six accessory setae. Basic seta of anterior sternite of mesothorax and metathorax medium to large; surface with three major accessory setae. Mesosternite and metasternite basic seta size large; surface with three small accessory setae. Membrane sculpture extremely fine or absent. Seta PII-P size on abdominal terga 1 to 8 small to medium-small; size of accessory setae on row in front of basic anterior row of setae medium ot terga 1 to 8; pointed sculpture on anterior band on 10% of band surface of terga 1 to 8; tergum 10 with three major and two to 22 minor accessory setae. Epipleuron of segments 1 to 8 divided. Hypopleuron of segments 1 to 8 with 12 to 16 accessory setae. Sternite of segment 1 with eight to 16 accessory setae, segments 2 to 7 with 30 to 40, segment 8 with 40 to 50, and segment 9 with 15 to 25, and segment 10 with five major and 15 minor accessory setae. External poststernite on segment 1 with seven, and on segments 2 to 7 with 10 accessory setae; pointed sculpture on segments 2 to 7 present. Internal poststernite on segments 2 to 7 with six accessory setae.

Second Instar Larvae. Description.- Size large 9 to 15 mm. Color as for the first instar larva. Membrane sculpture very fine or absent.

Head. Frontale seta EMP size small to medium-small; surface with three accessory setae; antero-discal field of sculpture present. Parietal seta VMA large; dorso-discal surface with seven to 10, and lateral surface with seven to eight accessory setae; size of accessory setae between DMM-P and DI-A small; dorsally sculpture present near lateral margin, and pointed sculpture present on 1 to 5% of surface, ventrally sculpture along lateral margin, and discal sculpture on both sides of system VMM and VMP convex.

Mouthparts. Posterior margin of mandible retinaculum without or with suggested teeth. Stipes ventrally with three antero-discal and few postero-lateral accessory setae, and dorsally, in one member, with few postero-lateral accessory setae, ; pointed sculpture on dorsal external 0.5 of surface or restricted basally. Mentum with nine to 10 dorso-lateral and one antero-lateral accessory setae; size of dorso-lateral accessory setae medium.

Thorax. Pronotum on each half with 95 and on pronotal epipleuron with 12 to 14 accessory setae; size of accessory setae on row anterior to anterior row of basic setae small to medium, size of largest accessory seta on epipleuron large; 10 to 30% of surface of pronotal disc with sculpture, without or with pointed sculpture on 5% of disc surface, pronotal epipleuron without sculpture. Proepisternum size of basic seta medium-small; surface with seven accessory setae; sculpture absent. Size of major seta of anterior sternite

(AS) medium. Prosternum with 10 accessory setae of posterior band medium.

Mesonotum on each 0.5 with 60 to 70, and mesonotal epipleuron with 7 to 15 accessory setae; size of accessory setae of row behind posterior row of basic setae small to medium, size of major accessory setae on mesonotal epipleuron small to medium-small; sculpture on disc present on 20 to 100% of surface, pointed sculpture near suture present on 40% or absent, and on disc laterally on 5 to 60% of disc surface, and on anterior band absent or on 50% of band surface, no sculpture on mesonotal epipleuron. Mesepipleuron with 10 to 16 accessory setae; size of major accessory setae medium. Mesepisternum with three to six accessory setae; sculpture with very scattered fine points. Mesepimeron with five to 10 accessory setae; no sculpture. Anterior pleurite (AP) without sculpture. Anterior sternite (AS) basic seta size medium to large; surface with two or three accessory setae. Mesosternite basic setae size large; surface with three small accessory setae. Metathorax as mesothorax.

Membrane sculpture absent or extremely fine.

Abdomen. Seta PII-P on terga 1 to 8 small to medium-small; surface with 40 accessory setae on each discal 0.5; size of major accessory setae on row behind posterior row of basic setae very large, and size of accessory setae in front of anterior row of basic setae medium; all terga covered entirely with sculpture, pointed sculpture on anterior and posterior bands on 10% of band surface; urogomphi of tergum 9 without or with raised setigerous punctures on internal margin; size of seta MPP-E small to medium-small; urogomphus with 15 to 25 major accessory setae (Fig. 96b); size of minor accessory setae very small to extremely small; pointed sculpture on anterior band on 10% of surface; seta PI-P size on tergum 10 large, and seta AM-P size large to very large; tergum 10 with three major and 20 to 25 minor accessory setae; sculpture single-pointed or multi-pointed, points fine or better defined. Epipleuron of segments 1 to 8 divided in two; segments 2 to 8 with 12 to 14 accessory setae. Hypopleuron on segments 1 to 8 with 12 to 16 accessory setae; size of major accessory setae very large and minor ones medium. Sternite on segment 1 with eight to 16 accessory setae, on segments 2 to 7 with 30 to 40, on segment 8 with 40 to 50, on segment 9 with 15 to 25, and on segment 10 with five major and 15 minor accessory setae; size of accessory setae small; sculpture single-pointed on first few segments, then more multi-pointed. External poststernite on segment 1 with seven, and on segments 2 to 7 each with 10 accessory setae; pointed sculpture on segments 2 to 7 present. Internal poststernite on segments 1 to 8 each with six accessory setae.

Membrane sculpture absent or extremely fine.

Third Instar Larvae. _Diagnostic combination_.- Size large 15 to 23 mm. Parietal seta DI-A size medium-large.

Disc of pronotum with 100 to 130 and pronotal epipleuron with 30 to 40 accessory setae. Mesepimeron and metepimeron with 10 to 15 setae; basic seta size medium. Anterior pleurite (AP) of metathorax with 11 accessory setae. Mesosternite and metasternite with nine to 10 accessory setae. Size of abdominal setae AII and AIM on terga 1 to 8 large; disc of terga 1 to 8 with 30 to 50 accessory setae, tergum 10 with 24 minor accessory setae; sculpture of urogomphus on tergum 9 absent, or suggested, or made of fine points. Sternite on segment 1 with 20 to 55 accessory setae, on segments 2 to 7 with 90 to 150, on segment 8 with 50 to 130, and on segment 9 with 30 to 60 , and on segment 10 with six major accessory setae. External poststernite on segment 1 with 30 to 45 and on segments 2 to 7 with 35 to 55 accessory setae. Internal poststernite on segment 1 with 10 to 25, and on segments 2 to 7 with 20 to 25 accessory setae. Membrane sculpture absent.

Third _Instar_ _Larvae_. _Description_.- Size large, length 15 to 23 mm. Color as first instar larva.

Head. Frontale seta EA-E size small, and seta MP size very small; surface with seven accessory setae. Parietal seta DI-A size medium-large, and seta VMP-A size medium; sculpture on both sides of systems VMM and VMP defined or weak.

Mouthparts. Posterior margin of retinaculum without teeth or teeth barely suggested. External 0.5 of stipes dorsum without pointed sculpture or present on entire surface. Prementum with 12 to 17 dorso-lateral, and one to three antero-lateral accessory setae.

Thorax. Pronotum with 100 to 130, and pronotal epipleuron with 30 to 40 accessory setae; sculpture on disc on 1 to 5% of surface, pointed sculpture on 1% of surface. Proepisternum with 20 accessory setae. Proepimeron with two to 13 accessory setae.

Mesonotum with 90 to 110, pronotal epipleuron with 20 to 35, and posterior band without or with two accessory setae; size of setae on row behind posterior row of basic setae medium to large, sculpture on 20 to 40% of disc surface, pointed sculpture absent or present on 2 to 5% near suture, and on 1 to 15% laterally of disc surface, and on 50 to 100% of surface of posterior band surface. Mesepisternum with four to six accessory setae. Mesepimeron with basic seta size medium; surface with 10 to 15 accessory setae. Mesosternite with nine to 10 accessory setae. Metathorax as mesothorax except anterior pleurite (AP) with 11 accessory setae.

Abdomen. Tergal epipleuron on terga 1 to 8 narrow; elevated major setigerous punctures of urogomphus on tergum 9 in lateral view medium and in dorsal view small; size of setae AII and AIM on terga 1 to 8 large, and size of seta PII-P small to medium-small; disc of terga 1 to 8 with 80 to 100, and tergal epipleuron with 30 to 50, urogomphus of tergum 9 with 20 to 30 (Fig. 96b), and on tergum 10 with four major and 25 minor accessory setae; sculpture completely covering terga starting on tergum 1 or 2; pointed sculpture on terga 1 to 8 on anterior band on 50 to 100% of band surface, on posterior band absent, on anterior band of tergum 9 absent or on 50 to 100% of band surface, on urogomphus of tergum 9 sculpture absent, or suggested, or formed of fine points. Epipleuron of segments 2 to 8 with 30 to 45 accessory setae; sculpture on segment 1 absent, on segments 2 to 8 present, on segments 2 to 4 sculpture suggested to fine. Hypopleuron on segments 2 to 8 with 30 to 40 accessory setae. Sternite on segment 1 with 20 to 55 accessory setae, on segments 2 to 7 with 90 to 150, on segment 8 with 50 to 130, on segment 9 with 30 to 60 accessory setae, and on segment 10 with six major accessory setae; size of accessory setae on segments 2 to 7 medium; sculpture on segments 2 to 7 single-pointed or multi-pointed, looking like scales. External poststernite on segment 1 with 30 to 45, and on segments 2 to 7 with 35 to 55 accessory setae. Internal poststernite on segment 1 with 10 to 25, and on segments 2 to 7 with 20 to 25 aacessory setae.

Membrane sculpture absent.

Distribution.- Members of this genus are found from the British Isles to Kamchatka, and from Alaska to Newfoundland, from the southern edge of the tundra to the northern half of the warm temperate zone (Lindroth, 1954). I have seen some or numerous adults of all species described by Lindroth (1954). I examined four first instar, three second instar, and three third instar larvae of *B. quadricollis* from the junction of the Athabasca River with Highway 2, Alberta; six first instar, two second instar, and three third instar larvae of *B. multipunctata* from George Lake, Alberta; five second instar larvae of *B. julii* from three localities in Newfoundland, and two third instar larvae *B. julii* from two localities in Newfoundland.

3.5 Genus *Elaphrus* Fabricius

Elaphrus Fabricius 1775: 227. *Type species*.- *Elaphrus riparia* Linneus 1758: 407 (subsequent designation by Latreille 1810: 425). Lindroth 1961: 109.

Adults. *Diagnostic combination*.- Frons medial surface lower than eye margin, thus seemingly concave; eyes very large (Fig. 16); punctures unequally distributed dorsally, surface without punctures in many members strongly reflective (mirrors), frons medially with weak or well defined impression; punctures very dense and irregularly elongated when impression weak. Apical retinacular tooth of left mandible well removed from terebral tooth. Pronotum discal impression present though very weak in some members; pronotum with one seta only along lateral margin near postero-lateral angle. Proepisternal flange very wide. Sculpture of coxal cavities with relatively large points. Accessory setae present laterally, posteriorly and anteriorly on metasternum; alveolae convex laterally. Abdominal tergum 2 with two antero-medial ridges. Accessory setae present on sternum 7 and sterna 2 to 6 of males and females; punctures present laterally at least on segment 5. Elytral striae barely suggested, in some members, or absent; basal transverse stria ended at shoulder; discal and umbellical setigerous punctures surrounded by a weak or well defined circular structure (pit) or without it; at least surface with one strongly reflective surface (mirror); disc with three rows of setigerous punctures; punctures present on intervals 1, 2, 4, 6, and 8, and in pit; interval and pits in most members densely punctured; setigerous punctures in most members very enlarged (50 microns) or small (15 microns). Femur of foreleg with numerous setae (30 or more). Tibia of foreleg with setae of posterior internal row expanded near apex. Coxa of midleg with numerous setae. Femur of midleg with numerous setae (27 or more). Tibia of midleg with numerous setae (55 or more); anterior medial and internal, and posterior internal rows of setae expanded near apex. Coxa of hind leg with at least four setae (one postero-medial and many medium setae). Femur of hind leg with more setae (six or more). Tibia of hind leg with numerous setae (60 or more); external row of setae present; anterior medial and internal, and posterior internal rows of setae expanded near apex. Basal sclerite of stylus of females with dorso-lateral ridges, ridges with wide spinules. Apical sclerite of stylus without or with few (two to six) very small and stout spines along dorso-lateral ridges; apical setae without or with one or two very small setae.

Adults. Description.- Small to medium beetles: body length from 6 to 10 mm. Pronotum narrow, eyes prominent, thus cicindeloid-like (Fig. 16). Upper surface dark or brilliant copper or green, ventral surface darker. Pores in punctures small.

Head. Frons lower than dorso-lateral margin of eyes; eyes very prominent; punctures unequally distributed, surface without punctures in many members, without sculpture and very reflective (mirrors); fronto-ocular sulcus indistinct, frontal impression indistinct or well defined (when indistinct, punctures in impressions denser and irregularly elongated); accessory setae present in some members on frons near eyes; cornea of eyes thick or thin, thickness of anterior and posterior cornea subequal or unequal; punctures dense or scattered; sculpture lines present at least in spots, alveolae flat to convex. Clypeus with two or four or more setae laterally on disc; punctures present, restricted baso-medially or on surface; punctures 15 to 20 microns in size, in contact or up to 60 microns apart, edge of punctures indistinctly or sharply defined up to 100% of circumference; sculpture lines absent medially in some members, or present on entire surface, alveolae flat to convex. Labrum sculpture lines present, alveolae flat to convex.

Antennae. Antennal scape 1.5 to 1.8 length of antennomere 2, antennomere 2 0.4 to 0.7 length of antennomere 3; antennomere 3 with dense pubescence, or with scattered small setae, or with few apical setae (Fig. 11 to 13); sculpture lines present,alveolae flat to convex.

Mouthparts. Grinding edge of right mandible 0.4 to 0.7 length of mandible, basal retinacular tooth single or double, terebral tooth prominent (Fig. 3 and 4); left mandible with weak or prominent molar and basal retinacular tooth, terebral tooth prominent or very prominent, apical retinacular well removed from terebral tooth. Sculpture on stipes present, alveolae flat or convex. Maxillary palpomere 1 narrow or wide (Fig. 7); palpomere 1 0.4 to 0.5 length of palpomere 2, palpomere 2 1.7 length of palpomere 3, palpomere 3 0.3 to 0.5 length of palpomere 4; sculpture lines present, alveolae flat. Galeomere 1 1.5 to 2.0 length of galeomere 2, galeomere 1 subequal or 1.5 length of maxillary palpomere 2, galeomere 2 0.7 length of maxillary palpomere 4. Length of sharp projection of lacinia 1.2 to 1.5 width of lacinia, length of spines on internal margin of lacinia subequal to 1.2 width of lacinia; spines alternatively small and smaller or subequal. Gula normally long or shorter, anterior expansion of submentum with six to eight major setae and without or with few minor very small setae; sculpture lines present, alveolae indistinctly or well defined, alveolae flat to convex at least at base. Mentum (Fig. 10) medial teeth length 0.5 ot 0.8 depth of memtum emargination, medial teeth emargination 0.2 to 1.0 length of tooth; mentum with two medial setae; sculpture lines present, alveolae flat to convex. Ligula barely to very prominent. Labial palpomere 1 0.7 to 0.8 length of palpomere 2.

Thorax. Pronotum margin very narrow; lateral bead complete between lateral angles or incomplete especially in sinuation; disc with at least one discal impression, weakly expressed in few members; setae of fringe of anterior and posterior margins scimitar-shaped, scimitar setae slightly enlarged or enlarged apically, fringe reaching or not reaching lateral angles, medial setae of fringe 0.5 or 1.0 length of lateral ones; one seta along lateral margin near posterior angle; accessory setae absent or present medially; punctures present unevenly distributed in some members; mirrors present on disc, punctures 12 to 50 microns in size, in some members up to 240 microns and in others up to 10 microns apart on disc, edge of puncture shallowly or sharply impressed up to 100% of circumference; sculpture lines absent or present in spots or on entire surface in some members, alveolae flat to convex, better impressed laterally. Proepisternal sulcus at junction of disc and flange very short; flange medium to large; punctures on disc 20 to 35 microns in size, punctures in contact or up to 140 microns apart, edge of punctures sharply defined on 50 to 100% of circumference; sculpture lines present, alveolae flat to convex. Proepimeron suture absent or indistinct, puncture size and density as proepisternum; sculpture as proepisternum except sculpture on posterior margin slightly transverse. Prosternum lateral margin slightly or deeply sinuate; setae shape of anterior margin as pronotum fringe except for females of one member with narrow setae; setae absent, or present apically, or on surface; punctures 12 to 35 microns in size, denser laterally where up to 60 microns apart, edge of punctures laterally on prosternum sharply defined on 50 to 70% of circumference, on disc less well defined; sculpture lines present, alveolae flat to convex, better impressed laterally, medially slightly transverse, sculpture of coxal cavities formed of larger points.

Scutellum without transverse ridge anteriorly (posteriorly without or with weak sulcus); lateral posterior ridge nearly reaching or reaching apex; punctures absent or present, puncture 20 to 30 microns in size, in contact or up to 120 microns apart, edge of punctures sharply defined on 30 to 50% of circumference; sculpture lines absent or present, alveolae flat to convex, alveolae indistinct or absent posteriorly and convex anteriorly, anterior alveolae in part slightly transverse. Mesepisternum discal ridge indistinct or absent; punctures 25 to 50 microns in size, in contact or up to 120 microns apart, edge of punctures sharply defined on 50 to 70% of circumference; sculpture lines present laterally, alveolae flat to convex and, in part slightly transverse. Mesepimeron punctures as mesepisternum but punctures less dense; sculpture as mesepisternum. Mesosternum postero-lateral ridge weakly developed or absent; accessory setae absent or present; punctures 25 to 50 microns in size, denser laterally up to 150 microns apart; sculpture lines absent or present, absent at base, alveolae flat to convex alveolae in many members with fine to large points along posterior edge medially and for others medio-anteriorly and laterally, sculpture at base formed of points.

Apico-lateral setae of metanotum small to very small; discal setae few. Metepisternum anterior sulcus indistinct or not developed; discal accessory setae absent or present; punctures 25 to 50 microns in size, in contact or up to 250 microns apart, edge of punctures indistinct or well defined up to 70% of circumference; sculpture lines present, alveolae flat to convex. Metepimeron well defined, metasternal accessory setae present on disc and, in most members on lateral and posterior surfaces, medial punctures with setae in most or in 20% of punctures, lateral punctures without setae or up to 90% of punctures with setae, punctures 25 to 50 microns in size, in contact or up to 150 microns apart, more scattered medially, edge of punctures sharply defined on 30 to 70% of circumference; sculpture lines present, alveolae flat to convex, alveolae indistinct in spots medially and well defined laterally, alveolae, in part, slightly transverse medially (internal to punctures in inverted V).

Abdomen. Tergum 2 with two medial ridges anteriorly;

tergum 7 with 13 to 25 large points along posterior margin of stridulatory scraper, points 25 to 35 microns apart; tergum 1 without setae, tergum 7 without setae or with setae along anterior margin, or with setae on entire surface, tergum 8 with numerous setae on entire surface; sculpture lines on tergum 8 present, alveolae flat or convex. Abdominal sternum 7 with two pairs or in one member with one pair of setae along posterior margin; sternum 7 with at least two accesory setae, setae dense on sterna 3 and 4, and also on sternum 5 and 6 of most members, setae in most members restricted between ambulatory setae, or in some members extended laterally into lateral punctate area; punctures present laterally on sterna 2 to 6, and in most members on sternum 7, punctures 25 to 50 microns in size, in contact or up to 100 microns apart, edge of punctures sharply defined on 30 to 70% of circumference; sculpture lines present, alveolae flat to convex, better impressed laterally, and slightly transverse medially.

Elytra. Striae barely traceable at base or absent. Base of stria 5 deeply impressed (Fig. 110 to 117). Basal transverse stria not extended beyond shoulder, there stria indistinct or deeply impressed. Surface with four rows of circular impressions (pits), pits (Fig. 131 to 136) delimited externally by punctures in semi-circular stria, or by depressions between intervals and pits, or by color outline (golden-copper band), or not delimited (details in puncture elongation pattern can suggest pits in _E_. _viridis_);

inside limits of pits two semi-circular ridges or one circular ridge, or no ridge; interior of pit with four or many more punctures arranged roughly concentrically; center of pit with setigerous punctures at center; pits restricted to intervals 3, 5, 7 and 9; interval 3 with five to six, interval 5 with four , interval 7 with four, and interval 9 with seven or eight setigerous pits; base of elytron with two non-setigerous punctures roughly in position of intervals 5 and 7. Setigerous punctures very large (45 to 55 microns) or in members of E. lapponicus small (15 to 20 microns). Scutellar setigerous punctures elevated but without the enlarged circular pit around. Strongly reflective surface (mirror) present, elytra with one to about 20 mirrors; mirrors between two pits of same interval, mirrors similar in width or with one or two major and wider mirrors. Punctures present in pits and in areas without mirrors (mostly in intervals 2, 4, 6 and 8), punctures in pits 20 to 45 microns in size, in contact or up to 30 microns apart, punctures outside pits same size, in contact to extremely far apart, edge of puncture indistinctly or sharply defined up to 100% of circumference. Surface of elytral articulation with mesothorax with two to six sharply defined, elongate and large punctures. Sculpture lines absent or present, alveolae flat to convex, mirrors without alveolae, sculpture best expressed in pits, intervals without sculpture, or alveolae present in spots or on entire surface (in some members alveolae present, but external surface with thin and very smooth outer layer, thus alveolae invisible under SEM). Epipleuron of elytron punctate on entire surface. Stridulatory file under elytron near apex indistinct (lines 3 microns apart) or well impressed (lines 4.5 to 7 microns apart) -- sound produced about same in composition and strength.

Wings. Venation very similar to members of other genera except that posterior end of oblongum not rounded but subangular.

Legs (Fig. 32). Coxa of foreleg without or with punctures, punctures 15 to 30 microns in size, in contact or up to 180 microns apart, edge of puncture indistinct or distinct up to 50% of circumference; sculpture lines present, alveolae flat or convex. Trochanter with one, two or three setae; sculpture lines present, alveolae flat and indistinct or well defined. Internal face of femur (Fig. 145 and 146) smooth, setae numerous (30 or more), postero-external row with five or more, postero-internal row with 9 or more, antero-external row present with four or more, and antero-internal row with six or more setae; sculpture lines present, alveolae flat or convex. Tibia (Fig. 145 and 146) without or with projections at base of apical spur and/or projection at base of posterior spur; postero-internal row of setae expanded toward apex, anterior internal fringe on 50 to 80% of tibia length, in one member with few setae behind fringe; sculpture lines present, alveolae flat to scale-like, and better impressed apically. Tarsomeres 1 to 4 or 1 to 3 of males with spongy pubescence ventrally; tarsomeres 1 to 4 each with four to 10 spinules and tarsomere 5 with two to 10 spinules ventrally; sculpture lines present, alveolae flat or convex.

Coxa of midleg with numerous setae (in addition two major ones); punctures 20 to 30 microns in size, 20 to 150 microns apart, edge of punctures sharply defined on 30 to 50% of circumference; sculpture lines present, alveolae flat to convex, and, in part, slightly transverse. Trochanter with one, two or three setae; sculpture as coxa except alveolae flat. Femur (Fig. 147 and 148) smooth along internal margin; surface with numerous setae (27 or more); sculpture lines present, alveolae flat or convex. Apico-internal angle of tibia of males with projection in most members (Fig. 150); surface setae numerous (55 or more) (Fig. 148 and 149), anterior medial row of setae with eight or more, and anterior internal with 10 or more setae, anterior medial and internal, and posterior internal rows of setae expanded apically; sculpture lines present, alveolae flat or convex apically. Tarsomeres 1 to 4 each with four to 14, and tarsomere 5 with two to 10 spinules ventrally; sculpture as femur.

Coxa of hind leg, in addition to large posterior seta with numerous setae (three to 40), setae distributed on entire surface or on inner 0.5 or more restricted near margin; 10 to 100% of punctures with setae, punctures 15 to 45 microns in size, in contact or up to 150 microns apart, edge of punctures indistinct or sharply defined on 30 to 70% of circumference; sculpture lines present, alveolae flat, and indistinct or well defined. Posterior basal face of trochanter with few spinules (about six); sculpture lines present, alveolae flat and, in part, slightly transverse. Femur with numerous setae (six or more); sculpture as trochanter. Tibia with external row of setae present; surface with numerous setae (50 or more), posterior internal, anterior medial rows with 14 or more setae, anterior medial and internal, and posterior internal rows of setae expanded apically; sculpture lines present, alveolae flat or convex, and better impressed apically. Tarsomeres 1 to 4 each with six to 24 and tarsomere 5 with two to 12 spinules ventrally; sculpture lines present, alveolae flat or convex.

Male genitalia. Baso-lateral and ventral surfaces thickly sclerotized and sharply separated from thinly sclerotized lateral sides; stylet of internal sac very large, and protruded well beyond basal orifice, posterior end of stylet flat and enlarged for muscle attachment; basal orifice open dorsally. Ventral portion of apical spatula without ventral hooks (Fig. 40).

Ovipositor. Dorso-lateral ridges of basal sclerite of stylus present, each ridge with spinules, ventro-apical surface of basal sclerite without or with spinules. Apical sclerite of stylet with two to six very small stout spines along dorsal ridges, apex without or with one very small or two very small or extremely small setae (Fig. 72 to 75).

First Instar Larvae. Diagnostic combination.- Nasale of frontale very prominent, teeth on nasale clearly separated into two groups by medial projection, teeth medium, very fine, or absent (Fig. 89b to 92b); seta EMP size very small to absent (setigerous pore present). Position of parietale pore VEP-A external to seta VEP-P, pore and seta of system VEM distant as pore VEM-A in front of posterior row of ocelli, angle formed by seta DI-A, and pores DI-P and DMP-E less open (about 130° or less); size of seta DEP and DI-A medium-small to large, seta VEP-P size medium to large, seta DMM-A size very small to medium, setae DMP-A, VMA and VMP-A size small to medium, and seta VEM-P size medium to large. Width of head at eye level relatively wider: PW/PML 1.26 to 1.76, and length of parietale along ventral midline relatively shorter: PML/PBW 0.75 to 1.06 except in E. ulrichi with 1.08 and 1.14. Basal internal margin of mandible enlarged so not continuous with apical cutting edge. Anterior seta of stipes along external margin in front of lacinia level. Lacinia very small or barely suggested. Ligula narrow and in many members collapsed. Size of proepisternal and proepimeral seta very small to small. Size of mesepipleural and metepipleural seta small to medium large. Size of setae AII and AIM of terga 1 to 8 very small to small. Internal poststernite with small to very small internal seta on terga 1 to 8. Sculpture on urogomphus of tergum single-pointed not scale-like.

First Instar Larvae. Description. Small to medium, body length 3 to 4 mm just after hatching and 6 to 7 mm when fully grown. Dorsally head capsule all pale, or mostly pale except near frontale suture, or pale laterally, or pale behind eyes and postero-laterally, or basally, and ventrally all pale or at base only.

Head. Nasale of frontale very prominent, teeth absent or present, teeth very fine, or fine or medium, teeth separated into two groups by medial projection (Fig. 89b to 92b); pore MMP-E external or internal to anterior end of egg-burster, and pore MA-I parallel or internal to seta MMA; seta EMP size very small or absent (setigerous pore present), and seta MP small to absent (setigerous pore present). Marginal convexity between neck and eye longer than or subequal to convexity posterior to neck; epicranial suture subequal to or as short as 0.2 length of antennal scape; seta DI-A posterior to or level with postero-lateral angle of frontale, system DMM normal or moved forward, thus seta DMM-P anterior to postero-basal angle of frontale, pore VEP-A external to seta VEP-P, pore and seta of system VEM distant, thus pore VEM-A in front of posterior row of ocelli, angle formed by setae DI-A, and pores DI-P and DMP-E less open (about 130° or less), triangle formed by setae DEP, VEP-P and VEM-P with anterior angle moderate (equilateral triangle) or angle very open; size of setae DEP and DI-A medium-small to large, seta DMM-A size very small to medium, setae DMP-A, VMA and VMP-A small to medium, seta VEM-P size medium to large; sculpture lines absent or present in spots, dorsally alveolae present on surface lateral portion (specifically different among many members), extended ventrally along lateral margin or just basolaterally, pointed sculpture dorsally absent or up to 50% of surface, extended or not ventrally up to 15% of surface.

Head proportions (Fig. 77) as follows: FW/OL 3.3 to 12.0, PL/OL 3.0 to 9.6, Fl/OL 2.4 to 9.2, Pl/PL 1.4 to 5.2, Pl/OL 4.4 to 6.2, FW/PL 1.1 to 1.6, PLP/PlP 1.2 to 2.4, PlP/PlA 2.2 to 13.0, PW/PML 1.2 to 1.76, PW/PlP 1.6 to 2.5, and PML/PBW 0.75 to 1.14

Antennae. Antennomere 3 1.5 length of antennomere 2.

Mouthparts. Base of mandible wide, internal basal margin not continuous with apical cutting edge (Fig. 80 and 81); posterior edge of retinaculum with fine or slightly coarser teeth, cutting edge without or with very fine or fine teeth. Stipes short 2.0 to 4.0 times as long as wide (Fig. 85); lateral margin of stipes behind posterior lateral seta interrupted by thinly sclerotized surface or not, margin near this surface projected outward or margin entire; setae on dorsal internal 0.5 moderately dense or denser (30 to 50), setae in apical 0.3 approximating one row or in two or more rows, ventral pores in basal 0.33 far apart or close--anterior pore nearly level with posterior one, anterior seta on external margin of stipes anterior to lacinia level; pointed sculpture on dorsal external 0.5 on surface, or more lateral. Lacinia very small (Fig. 85c); apical seta small, subequal to 0.5 length of seta on internal margin of stipes behind lacinia. Size of seta on galeomere 2 in apical 0.1 to 0.6. Maxillary palpomere 1 subequal to 1.5 length of palpomere 2. Ligula narrower, projection well defined or individually collapsed; size of antero-lateral spinule of prementum small to medium small.

Thorax. Pronotal seta size AII-E small to large, size MI and ME-I small to medium-small, and size of PII-P very small to medium-small; disc without or with sculpture up to 100% of surface, pointed sculpture absent or up to 5% of disc surface. Proepisternal and proepimeral seta size very small to medium small.

Mesonotal setae size AIM and AIE-I small to large, size of PIM-I and PIE-A small to very large, and size of PII-P small to medium-small. Sculpture lines present, alveolae absent or up to 60% of disc surface, pointed sculpture near suture absent or up to 30% and laterally from 5 to 35% of disc surface, and on posterior band absent or up to 100% of band surface. Mesepisternal seta size small to medium small. Anterior sternite seta size small. Mesosternite seta size medium small or medium. Metathorax as mesothorax.

Membrane ventrally and laterally with pointed sculpture on 15 to 90% of surface.

Abdomen. Size of setae AII and AIM on terga 1 to 8 small to medium-small, and size of seta PII-P of these terga very small to small, and size of seta AMP on tergum 9 small to medium-small; seta AIM of similar size on terga 1 to 8 or abruptly smaller from terga 5 to 8; sculpture single-pointed or multi-pointed on terga 1 to 8, single-pointed on urogomphus of tergum 9 and extended on entire surface or basal 0.5, and on tergum 10 sculpture single-pointed. Size of anterior seta of epipleuron on segments 1 to 8 medium to medium-large, and on segment 9 very small to medium small, seta in some members abruptly smaller starting at any segment from segment 1 to 8. Size of sternite seta on segments 2 to 7 medium-small to medium; sculpture multi-pointed, very fine to well defined on segments 2 to 7, and on segment 10 sculpture on entire surface or restricted basally. Size of anterior seta of external poststernite on segment 9 small to medium. Size of interior seta of internal poststernite on segments 1 to 8 very small to small, and on segment 9 very small to medium-small.

Membrane dorsally narrowly expanded baso-laterally, laterally expanded to very expanded, and ventrally restricted to expanded.

Second Instar Larvae. *Diagnostic combination*.- Size of accessory setae on frontale extremely small to absent (setigerous punctures present); anterior discal field of microsculpture not defined. Size of accessory seta between DMM-P and DI-A small or absent (setigerous punctures present); alveolae of microsculpture on both sides of systems VMM and VMP flat, indistinct or well defined. No accessory setae on ventral side of stipes either apico-medially or latero-posteriorly. Pronotum with 15 to 40, and pronotal epipleuron with two to seven accessory setae; size of major accessory setae on pronotal epipleuron very small to small. Prosternum with two accessory setae; size of accessory setae medium-small to medium-large. Mesonotum with 10 to 40, mesonotal epipleuron with one to five accessory setae; size of major accessory setae on mesonotal epipleuron very small to small. Mesepipleuron basic seta small to medium-large; size of major accessory setae very small to small. Mesepisternum with one accessory seta. Mesepimeron with one to four accessory setae. Size of major accessory setae in anterior pleurite of mesothorax very small to small. Anterior sternite of mesothorax with one accessory seta. Size of basic mesosternite seta medium to medium-large; surface without or with three accessory setae. Metathorax as mesothorax. Membrane clearly sculptured with points, points large to very fine. Size of setae on row in front of anterior row of basic setae small, tergum 10 without or with two major and without or with one to four minor accessory setae. Epipleuron of segments 1 to 8 not divided medially. Size of major accessory setae of hypopleuron of segments 1 to 8 medium-small to medium. Sternite on segment 1 with two to six, on segments 2 to 7 each with 10 to 20, on segment 8 with 10 to 22, on segment 9 without or with six or less, and on segment 10 with two or three major and three to six minor accessory setae. External poststernite on segment 1 with two to four, and on segments 2 to 7 each with 3 to 7 accessory setae; no sculpture. Internal poststernite on segment 1 without or with one or two, and on segments 2 to 7 each with one to four accessory setae. Membrane of abdomen as membrane of thorax.

Second Instar Larvae. Description.- Body length 7 to 9 mm when fully grown. Color as first instar in most members, except for members of *E. ulrichi* (described under this species).

Head. Teeth on nasale very small to medium; size of seta EMP on frontale absent (setigerous punctures present), or very small; size of seta MP absent (setigerous puncture present) to small; frontale with about five accessory setae; accessory setae barely visible or absent (setigerous punctures present); field of sculpture antero-medially absent. Size of seta DI-A on parietale small to medium, size of seta VMA small to medium; dorsal discal surface with few (zero to five) or more (five to seven), and along latero-ventral surface with three to nine accessory setae; size of accessory setae between DMM-P and DI-A absent (setigerous puncture present) or small, alveolae of microsculpture present laterally to baso-laterally on dorsal surface, and absent or very close to lateral margin on ventral surface, pointed sculpture absent or present up to 30% of dorsal surface and up to 5% of ventral surface, alveolae of fields on both sides of systems VMM and VMP flat.

Mouthparts. Posterior margin of retinaculum and cutting edge without or with barely suggested irregular teeth. Ventral surface of stipes apico-medially and postero-laterally, and postero-laterally on dorsal surface without accessory setae; pointed sculpture on external 0.5 of dorsal surface on or restricted baso-laterally. Size of mentum antero-lateral basic seta small; dorso-lateral surface with five to fifteen, and antero-lateral surface with one to three accessory setae; size of latero-basal accessory setae small to medium.

Thorax. Disc of pronotum with 15 to 45, and pronotal epipleuron with two to seven accessory setae; size of accessory setae on row behind to posterior row of basic setae small to medium-small, and size of major accessory setae on pronotal epipleuron very small to medium-small; microsculpture on disc absent or present up to 100% of surface, pointed sculpture absent or up to 5% of surface, sculpture on pronotal epipleuron absent or pointed. Size of proepisternal basic seta very small to medium; surface with five to seven accessory setae; microsculpture absent or single-pointed. Size of proepimeral basic seta very small to small; microsculpture absent or single-pointed and multipointed. Prosternite with two accessory setae; size of major accessory setae medium-small to medium.

Disc of mesonotum with eight to 40, and mesonotal epipleuron with one to five accessory setae; size of accessory setae on row behind posterior row of basic setae small to medium-large, and size of major setae on mesonotal epipleuron very small to small; microsculpture absent or present on up to 100% of disc surface, pointed sculpture absent or present near suture up to 30%, and laterally up to 35% of disc surface, and on anterior band up to 100% of band surface, sculpture on mesonotal epipleuron absent or present and single-pointed. Size of basic mesepipleural seta medium-small to medium-large; surface with one to nine accessory setae; size of major accessory setae very small to small; microsculpture absent or present and single-pointed or multi-pointed. Mesepisternum with one accessory seta; microsculpture absent or single-pointed and multi-pointed. Mesepimeron with one two or four accessory setae; microsculpture as on mesepisternum. Size of major accessory setae of anterior pleurite of mesothorax very small. Anterior sternite of mesothorax with one accessory seta. Size of basic seta of mesothorax medium-small to medium; surface without accessory setae. Metathorax as meosthorax.

Membrane sculpture clearly developed, pointed sculpture very fine to large.

Abdomen. Urogomphus of tergum 9 without internal knobs; size of seta MMP-E on urogomphus of tergum 9 very small or small, and of setae PI-P and AM-P on tergum 9 medium-small to large; discs of terga 1 to 8 each with 15 to 40 accessory setae, and tergum 9 with five to 25 major (Fig. 98b and 99a), and on tergum 10 without or with two major and without or with one to four minor accessory setae; size of accessory setae on row behind posterior row of basic setae medium-small to very large, and size of those in front of anterior row of basic setae small to medium-small, size of minor accessory setae on urogomphus of tergum 9 extremely small or very small; posterior accessory setae on urogomphus of tergum 9 lateral or dorso-medial in position, size of seta very small to large, and seta subequal or unequal in size to external discal seta; microsculpture single-pointed or multi-pointed, sculpture extended completely on disc starting on tergum 1, 2 or 4, or sculpture very restricted on all terga, pointed sculpture absent or present on anterior band, sculpture absent or present on posterior band on 5, 10 or 100% of band surface, pointed sculpture on anterior band of tergum 9 absent or on 10, or 100% of band surface, sculpture on urogomphus of tergum 9 scale-like, or single-pointed on entire surface or in basal 0.5 of urogomphus surface, on tergum 10 sculpture single-pointed or multi-pointed. Epipleuron of segments 1 to 8 entire; surface with eight to 30 accessory setae. Hypopleuron of segments 1 to 8 each with four to 20 accessory setae; size of major accessory setae small to medium, and of minor ones small to medium-small. Sternite of segment 1 with two to four accessory setae, of segments 2 to 7 each with 10 to 20, of segment 8 with 10 to 22, of segment 9 without or with two to six, and of segment 10 with two to three major and three to six minor accessory setae; size of accessory setae on segments 2 to 7 small to medium-small; pointed sculpture absent from segments 1 to 7, absent or present on segment 8 up to 15% of disc surface, and present on segment 9 on 15 or 30% of surface, and on tergum 10 present on entire surface or restricted basally. External poststernite on segment 1 with two to four, and on segments 2 to 7 each with three to 15 accessory setae; sculpture absent. Internal poststernite on segment 1 without or with one to two accessory setae, and on segments 2 to 7 with one to four accessory setae.

Membrane sculpture of abdomen as thorax.

Third Instar Larvae. Diagnostic combination.- Seta MP on frontale absent (setigerous puncture present) or very small. Size of seta VEP-P on parietale medium to large. Size of accessory latero-basal seta on prementum small to medium-small. Pronotal disc with 14 to 40, and pronotal epipleuron with three to 12 accessory setae. Proepisternum basic seta very small to medium-small. Prosternite with four accessory setae. Mesonotal epipleuron with one to five accessory setae; size of major accessory setae very small to medium-small. Mesepisternum without or with one to 12 accessory setae. Size of basic mesepimeral seta very small to medium-small; mesepimeron with one to four accessory setae. Mesosternite without or with three accessory setae. Metathorax as mesothorax except anterior pleurite with three accessory setae. Tergal epipleuron on segments 1 to 8 with five to 25 accessory setae, tergum 10 with one to nine minor accessory setae. Sternite on segment 1 with two to 18 accessory setae, on segments 2 to 7 each with 12 to 38, on segment 8 with 14 to 40, on segment 9 without or with two to 12, and on segment 10 with two to five major and with or without two to 12 accessory setae; size of accessory setae on segments 2 to 7 small to medium-small. External poststernite on segment 1 with three to 15, and on segments 2 to 7 each with four to 20 accessory setae. Internal poststernite on segment 1 with one to five, and on segments 2 to 7 each with one to seven accessory setae. Membrane sculpture clearly defined, though in some members pointed sculpture very fine.

Third Instar Larvae. Description.- Body length of fully grown larvae 11 to 15 mm. Color as first instar larva on the head, urogomphus in some members sharply patterned; color of members of E. ulrichi very different and described under that species.

Head. Size of basic frontale seta EA-E very small to medium-small, and of seta MP absent (setigerous puncture present) or very small; surface with seven to nine accessory setae. Size of basic parietale seta VEP-P medium to large; alveolae of microsculpture on both sides of systems VMM and VMP weakly defined.

Mouthparts. Mandible cutting edge with trace of teeth. Pointed sculpture on external 0.5 of dorsal side of stipes on entire surface or more impressed basally. Prementum with two to 15 accessory setae dorso-laterally on each side, and with one to three accessory setae antero-laterally; size of postero-lateral accessory setae small to medium-small.

Thorax. Pronotal disc with 15 to 40, and pronotal epipleuron with two to 12 accessory setae; size of major accessory setae on pronotal epipleuron small to medium; microsculpture absent or present on 5% of surface. Size of prosternal basic seta very small to medium, surface with seven to 25 accessory setae. Prosternite with four accessory setae; size of accessory setae on posterior band very small to medium-large.

Mesonotal disc with 25 to 100, and mesonotal epipleuron with one to nine accessory setae, and posterior band without or with one to 15 accessory setae; size of major accessory setae on row behind posterior row of basic setae small to medium-large and size of major accessory setae on mesonotal epipleuron very small to medium-small; microsculpture absent or present on up to 100% of disc surface, pointed sculpture absent or present near suture up to 10%, and laterally up to 20% of disc surface, and absent or present up to 100% of anterior band surface. Mesepipleuron without or with one to 12 accessory setae. Size of basic mesepimeral seta very small to medium. Anterior sternite of mesothorax with small to medium basic setae. Metathorax as mesothorax except metepimeron with one to four accessory setae, and anterior pleurite with one to three accessory setae; size of major accessory setae of anterior pleurite extremely small to medium. Membrane sculpture clearly defined, pointed sculpture very fine to large.

Abdomen. Tergal epipleuron on segments 1 to 8 narrow or very explanate; knobs of urogomphus on tergum 9 absent along internal margin, in dorsal view very small to large, and in lateral view virtually absent to large (Fig. 97, 98c, 99b, 100b, 101b, and 103b). Size of basic setae AII and AIM on terga 1 to 8 medium-small to large, and of PII-P absent (setigerous puncture present) or present and up to medium-small; discs of terga 1 to 8 each with 17 to 140, tergal epipleuron on terga 1 to 8 each with five to 25, urogomphus on tergum 9 with seven to 30, and tergum 10 without or with four major and one to nine minor accessory setae; size of major accessory setae on row behind posterior row of basic setae medium-small to very large; microsculpture on disc of tergum starting from tergum 1, 2 or 4, or very restricted on all terga, pointed sculpture absent or present on up to 100% of anterior band surface, sculpture on urogomphus of tergum 9 absent or present, points single or scale-like. Epipleuron of segments 1 to 8 each with 8 to 40 accessory setae; sculpture on segments 1 and 9 absent or present, and on segments 2 to 8 absent or developed. Hypopleuron on segments 1 to 8 each with eight to 50 accessory setae; size of major accessory setae medium-small to medium. Sternite on segment 1 with two to 20 accessory setae, on segments 2 to 7 each with 12 to 40, on segment 8 with 15 to 40, on segment 9 without or with two to 12 and on segment 10 with two to five major and without or with two to 12 minor accessory setae; size of accessory setae on segments 2 to 7 small to medium-small; type of sculpture on segments 2 to 7 multi-pointed or in one member single-pointed, points very indistinct to well defined, in some members microsculpture lines clearly suggested. External poststernite on segment 1 with three to 15, and on segments 2 to 7 each with four to 20 accessory setae. Internal poststernite on segment 1 with one to five accessory setae, and on segments 2 to 7 each with one to seven.

Membrane sculpture clearly defined as on thorax, but in some members sculpture absent ventrally.

Distribution.- Members of this genus occur across the northern hemisphere from the southern edge of tundra regions to the southern half of the warm temperate zone (Morocco, southernmost California, northernmost Florida).

3.5.1 Key to Subgenera of Elaphrus Fabricius

Adults

1. Fringe of setae of posterior margin of pronotum extended to baso-lateral angle (Fig. 20 to 25); suture between proepisternum and proepimeron not evident; tarsomeres 1 to 3 of males slightly expanded and with spongy pubescence ventrally or not enlarged and without spongy pubescence 2

1'. Fringe of setae of posterior margin of pronotum terminated near middle of baso-lateral impression or at its beginning, clearly terminated before hind angle (Fig. 17 to 19); suture between proepisternum and proepimeron evident; tarsomeres 1 to 4 of males slightly expanded and with spongy pubescence on ventral surfaces 3

2.(1). Clypeus with four setigerous punctures (some individuals with five or six); disc of prosternum and process of mesosternum with setae; trochanter of foreleg and midleg with three setigerous punctures; setae on entire surface of coxa of hind leg ....Elaphrus Fabricius p.271

2'. Clypeus with two setigerous punctures; disc of prosternum and process of mesosternum asetose; trochanter of foreleg with two setigerous punctures, and of midleg with one or two; setae on coxa of hind leg on inner 0.5 of surface ....Elaphroterus Semenov p.299

3.(1'). Maxillary palpomere 3 0.5 length of palpomere 4; setae on disc of prosternum and laterally on metasternum; punctures in pits few (one to six) and irregularly arranged (Fig. 131); microsculpture of elytra widespread with alveolae very convex. ....Arctelaphrus Semenov p.135

3'. Maxillary palpomere 3 0.3 length of palpomere 4; setae absent from disc of pronotum and lateral surface of metasternum; punctures in pits denser (eight or more) and more regularly distant from one another (Fig. 132 to 136); microsculpture alveolae convex in spots only (pit ridges especially). ....Neoelaphrus Hatch p.163

Larvae

1. Head elongate: lateral convexity in front of neck longer than one behind neck (Fig. 89a and 90a); epicranial suture 0.67 or 1.0 length of antennal scape; teeth on nasale medium and little separated by rather small medial projection, nasale markedly projected (Fig. 89b to 90b); maxillary palpomere 1 1.5 (I L and II L), or 1.2 (III L) length of palpomere 2; baso-ventral pores of stipes distant, internal pore distinctly anterior to external (Fig. 85b). 2

1'. Head short: lateral convexity in front of neck subequal to one posterior to neck (Fig. 91a and 92a); epicranial suture 0.6 or less than length of scape; teeth of nasale small to absent and well separated by large medial projection, nasale extremely projected (Fig. 91b and 92b); maxillary palpomere 1 1.0 (I L), or 0.8 (II L), or 0.7 (III L) length of palpomere 2; baso-ventral pores of stipes near one another, internal one slightly anterior to external (Fig. 83b). 3

2.(1). Stipes with unsclerotized band behind postero-lateral seta (Fig. 83b); pronotal setae MI and

ME-I and anterior epipleural seta of abdominal segment 8 small, mesonotal and metanotal seta PII-P very small, and anterior seta of external poststernite of segment 9 very small.

......................Arctelaphrus Semenov p.135

2'. Stipes with external surface sclerotized (Fig. 85b); pronotal setae MI and ME-I, anterior epipleural seta of abdominal segment 9 and mesonotal and metanotal seta PII-P medium-small, and anterior seta of external poststernite of segment 9 medium. ....Neoelaphrus Hatch p.163

3.(1'). Teeth of nasale absent or very fine, slightly extended anteriorly on medial projection (Fig. 91b); pointed sculpture on 30% of posterior band of mesonotum and metanotum. Internal seta of internal poststernite of segments 1 to 9 very small. ....Elaphrus Fabricius p.271

3'. Teeth of nasale small, and, in part, extended anteriorly along medial point (Fig. 92b); pointed sculpture over 50 to 100% of posterior band of mesonotum and metanotum surface. Internal seta of internal poststernite on segments 1 to 8 small and on segment 9 medium-small.

......................Elaphroterus Semenov p.299

3.5.2 Subgenus Arctelaphrus Semenov

Arctelaphrus Semenov 1926: 39. Type species.- Elaphrus lapponicus Gyllenhal 1810: 8, monobasic; designated by Semenov 1926: 39. Lindroth 1961: 111.

Adults. Diagnostic combination.- Maxillary palpomere 3 0.5 length of palpomere 4; galeomere 1 subequal to maxillary palpomere 2. Flange of proepisternum medium. Postero-lateral ridge of mesosternum slightly developed. Setigerous punctures in intervals 3, 5 and 7 small (20 microns), remainder large (40 microns). Pits on elytron with few irregularly arranged punctures; lateral ridges in pits very slightly convex. Posterior spur of tibia of foreleg anterior to base of antennal cleaner; anterior lateral row of femur with nine setae; fringe (anterior internal row) followed by about eight setae; tarsomere 5 with 10 spinules. Tarsomeres 1 to 4 of midleg each with 14 and tarsomere 5 with 10 spinules. Coxa of hindleg with 10 setae on internal 0.5 of coxal process; anterior medial and internal rows of tibia respectively with 37 and 46 setae; tarsomeres 1 to 4 each with 24 and tarsomere 5 with 12 spinules ventrally.

Adults. Description.- Head slightly narrower than pronotum. Dorsal surface especially of elytra with very convex alveolae of microsculpture.

Head. Ommatidia of eyes of similar diameter on the anterior and posterior surfaces.

Mouthparts. Grinding edge 0.67 length of right mandible (Fig. 3); basal tooth of retinaculum double humped; anterior retinacular tooth distinctly anterior to terebral tooth. Spines on lacinia internal margin alternatively small and smaller. Maxillary palpomere 3 0.5 length of palpomere 4. Galeomere 1 subequal to maxillary palpomere 2. Ligula very prominent. Mentum with eight large setae and/or very small accessory setae.

Thorax. Lateral margin of pronotum beaded; surface of disc with one impression. Fringe of setae along anterior and posterior margin not extended to lateral angles. Suture between proepisternum and proepimeron indistinct; internal flange medium. Lateral margin of prosternum not strongly constricted; disc and apophysis with setae; scimitar-shaped setae of fringes relatively narrow. Discal ridge of mesepisternum slightly developed. Postero-lateral ridge of mesosternum slightly developed; process without setae. Apico-lateral setae of metanotum small. Anterior ridge of metepisternum indistinct. Setae on side of metasternum in 20% of punctures.

Abdomen. Tergum 7 without setae. Sterna 2 to 6 each with 20 to 30 setae on disc, setae on sternum 7 numerous.

Elytra. Striae indistinct at base (Fig. 110). Transverse basal stria distinct at shoulder. Discal setigerous punctures very small (20 microns). Umbilical and scutellar setigerous punctures large (40 microns). Large punctures on elytral articulation distinct (five or six).

Pits with few irregularly arranged punctures; lateral ridges in pits indistinct.

Legs. Tibia of foreleg with posterior spur in front of base of antennal cleaner; tarsomeres 1 to 4 of males with spongy pubescence ventrally. Trochanter with two setae. Femur with about 70 setae; anterior lateral row with nine setae. Posterior medial row of setae of tibia with about 12 setae in both sexes; fringe (anterior internal row) of tibia 0.5 length of tibia with about eight posterior setae; tibia with about 34 setae. Tarsomeres 1 to 4 each with eight and tarsomere 5 with 10 spinules.

Coxa of midleg with few accessory setae. Trochanter with one seta (rarely with two). Femur with about 75 setae. Tibia with about 80 setae; anterior external row with 3 setae. Tarsomeres 1 to 4 each with 14, and tarsomere 5 with 10 spinules.

Coxa of hind leg with about 10 accessory setae on internal 0.5 of coxal process; all punctures with setae except those on lateral portion of coxa. Femur with about 20 setae. Tibia with about 125 setae; anterior medial and internal row with 35 and 45 setae respectively. Tarsomeres 1 to 4 each with 24 and tarsomere 5 with 12 spinules.

Male genitalia. Dorso-posterior portion of internal sac with two very large scales.

Ovipositor. Basal sclerite of stylus with some very small spines ventrally; apical sclerite with few stout dorso-lateral spines, and apex with two very small setae

(Fig. 72).

First Instar Larvae. *Diagnostic combination*.- Teeth on nasale large; medial projection small. Lateral convexity on side of parietale anterior to neck longer than one posterior. Epicranial suture as long as or longer than antennal scape. External lateral side of stipes with unsclerotized band behind posterior seta. Anterior seta of external poststernite on segment 9 very small to small.

First Instar Larvae. *Description*.- Body length medium, head width 0.6 mm. Head paler laterally and ventrally, urogomphus of tergum 9 pale at base.

Head. Nasale markedly projected; teeth on nasale separated by small medial projection; teeth large; seta MMP-E internal to egg-burster anterior end, pore MA-I in front of seta MMA. Head elongate: lateral convexity between eye and neck longer than convexity posterior to neck; epicranial suture subequal to or longer than antennal scape; seta DI-A behind baso-lateral angle of frontale, angle formed by seta DI-A and pores DI-P and DMP-E open (about 110 to 130°), and system DMM with seta DMM-P level with baso-lateral angle of frontale.

Mouthparts. Stipes short, about 2.0 to 2.5 times longer than wide; external lateral side of stipes with unsclerotized band behind posterior seta; dorsal setae on internal 0.5 moderately dense (about 30 setae), setae in apical 0.3 approximating one row; two posterior pores on ventral side distant from each other and interno-anterior pore well ahead of posterior one. Size of seta on galeomere 1 very small to small, microsetae along internal side of galeomere 2 in basal 0.6.

Thorax. Mesonotal setae AIM and AIE-I medium, setae PIM-I and PIE-A very large, and setae PII-P very small to small; pointed sculpture absent from basal band. Metathorax as mesothorax.

Abdomen. Seta AIM on terga 1 to 8 of similar size. Size of sternite setae on segments 2 to 7 medium. Size of anterior seta of external poststernite of segment 9 very small to small. Size of internal seta of internal poststernite of segments 1 to 9 very small.

Second Instar Larvae.- Larval stage not seen but very briefly described by Luff (1976) for the very similar third instar larva. Head width 0.8 mm. I assume this instar, as nearly all members of Elaphrus can be recognized by smaller knobs of urogomphus (about 0.5 size of third instar).

Third Instar Larvae. Diagnostic combination.- Pronotum and tergum 8 in part orange, other terga and nota brown (from Luff (1976), as my specimen was too teneral for interpretation). Meshes of microsculpture extended on entire dorsal surface of parietale, and pointed sculpture on 70% of dorsal surface. Antennae notably shorter than head (Fig. 89). Disc of pronotum with 14 accessory setae and about 70 accessory pores (with microsetae). Anterior pleurite of metathorax with three to four accessory pores; size of major accessory setae medium-small. Proepisternum with 15 accessory setae, and proepimeron with 10 accessory pores. Terga 2 to 8 without pointed sculpture; sternite of segment 1 with two accessory setae; sculpture on sternite of segments 2 to 7 single-pointed, and of segment 9 meshes distinct.

Third Instar Larvae. Description.- Head width 1.1 mm. Head, pronotum and tergum 8, in part, orange, remaining nota and terga brown.

Head. Size of basic seta MP of frontale very small. Size of basic seta DEP medium-small on parietale; surface with five to seven accessory setae near system DMM on dorsal side; triangle formed by setae DEP, VEP-P and VEM-P equilateral; meshes of microsculpture extended over dorsal surface, and pointed sculpture on 70% of dorsal surface.

Mouthparts. Prementum dorso-laterally without or with one or two setae, and antero-laterally with one accessory seta.

Antenna. Clearly shorter than head.

Thorax. Basic setae MI and ME-I on disc of pronotum small; disc with 14 and pronotal epipleuron with two accessory setae; major accessory setae on row behind posterior row of basic setae small; meshes of microsculpture on entire surface of disc. Proepisternal basic seta small; surface with 15 accessory setae. Proepimeral basic seta very small to small; surface with about 10 accessory pores. mesonotum with 16 accessory setae and about 40 accessory pores; Major accessory setae on row behind posterior row of basic setae medium-small; meshes of microsculpture on entire surface of disc, pointed sculpture absent from anterior band. Mesepipleuron with two accessory setae; size of major accessory setae medium. Mesepimeron with medium-small basic seta. Metathorax as mesothorax except anterior pleurite with very small major accessory seta.

Abdomen. Knobs of urogomphus of tergum 9 medium in size (fig. 97); basic seta PI-P on tergum 10 medium, seta MPP-E on tergum 9 small; disc of terga 1 to 8 each with about 37 accessory setae, epipleuron of terga 1 to 8 each with 10, urogomphus of tergum 9 with six to seven major, and tergum 10 with three minor accessory setae; sculpture absent from urogomphus of tergum 9, pointed sculpture absent from anterior and posterior bands of terga 1 to 9. Epipleuron of segments 2 to 8 each with 18 accessory setae. Hypopleuron of segments 1 to 8 each with 19 accessory setae; major accessory setae medium; no sculpture on surface. Sternite of segment 1 with two accessory setae, of segments 2 to 7 each with 22, of segment 8 with 30, of segment 9 with nine, and of segment 10 with three major and five minor accessory setae; sculpture on segments 1 to 8 single-pointed rarely with two or three points, on segment 9 meshes defined. External poststernite of segment 1 with one, and of segments 2 to 7 each with two accessory setae.

Membrane sculpture very faintly impressed or absent.

3.5.2.1 Elaphrus lapponicus Gyllenhal

Diagnostic combination.- Setigerous punctures on intervals 3, 5 and 7 small (15 to 20 microns). Disc of prosternum with setae, intercoxal process asetose; alveolae of microsculpture very convex and widespread over elytra; pits clearly outlined with punctures, each with few irregular punctures (fig. 118 and 131).

3.5.2.1.1 Elaphrus lapponicus lapponicus new status

Elaphrus lapponicus Gyllenhal 1810: 8. Type locality.- Abisko, Sweden designated by Lindroth 1961: 111; type in Goteborg Museum; seen by Lindroth (1961). Lindroth 1961: 111.

Elaphrus elongatus Fischer von Waldheim 1828: 266. Type locality.- Kamchatka, USSR; type at Zoological Museum, University, Helsinki; seen by Lindroth (1961). Lindroth 1961: 111.

Elaphrus obscurior Kirby 1837: 63. Type locality.- Latitude 65o-- according to Lindroth (1961) near Great Bear Lake; Type in British Museum of Natural History, London, England; seen by Lindroth (1961). Lindroth 1961: 111.

Adults. Diagnostic combination.- Specimens of this subspecies are recognized by their smaller size: elytra length (EL) of most specimens less than 5.4 mm, and by relatively wider head and longer pronotum; means of the following ratios were significantly different from *E. l. obliteratus*: PW/HW less than 1.05, EL/HW less than 2.32, EW/HW less than 0.830, and PL/EL more than 0.390. For details, see Table 1.

Adults. Description.- Black with metallic luster, dull; meshes of microsculpture dense, convex; reflections varied from black to brilliant green and copper; intervals bluish, green, golden, or black; pits in some specimens very contrasting, or in most specimens not so. Body especially narrow at shoulder.

Frontal impression of head indistinct or well delimited. Pronotum with one discal impression on each side. Postero-lateral ridges of mesosternum slightly impressed. Setae in about 20% of punctures laterally. Scraper plates of stridulatory organ on tergum 7 with 20 to 25 sharp teeth approximately 25 microns apart. Punctures of abdomen laterally on sterna 3, 4, 5 and 6. Pits on elytra barely or clearly impressed; lateral ridges in pits absent to clearly outlined. Ridges of stridulatory file subapically beneath elytra, 4 microns apart. Apex of median lobe of male genitalia in dorsal view with sharp point on right side near base of apical spatula (Fig. 40b), in lateral view spatula moderately expanded and slightly bent ventrally; both right and left paramere wide with short setae extended in apical third; internal sac as in Fig. 40a .

Integument sculpture. Puncture size small (20 microns) on scutellum and all coxae, medium (25 to 30 microns) on dorsal surface, and ventrally on sterna, and large (30 to 40 microns) on pleura and laterally on abdominal sterna. Punctures indistinctly delimited on clypeus and elytra, otherwise sharply delimited on 30 to 67% of puncture circumference. Punctures quite dense (25 to 50 microns apart) except on scutellum, elytra, medially on thoracic sterna and coxae where more scattered.

Alveolae of microsculpture absent or very indistinctly outlined on scutellum and base of mesosternum, convex on abdominal sterna, and on metepisternum, and flat on remaining sclerites.

Measurements and proportions.- See Table 1.

Variation.- Only two composite samples were studied. Specimens from Scandinavia are generally larger with elytral features less well impressed. The pronotum is relatively wider in Scandinavian specimens; thus mean of ratio PW/EL significantly larger than means of the mainland North American sample, while the pronotum length is relatively larger in the North American sample. Thus the mean of ratio PL/PW is significantly larger than in Scandinavia.

Third Instar Larvae. Diagnostic combination.- Head, pronotum and most of tergum including base of uromgomphi orange, and meshes formed by lines of microsculpture on disc of terga characterize this species.

Third Instar Larvae. Description.- Head (except near frontale where darker), disc of pronotum and mesonotum and most of tergum 9 including base of urogomphi orange and remainder black or dark brown and very dull (preserved specimens tend to fade to brown) (Luff, 1971 and Lindroth, 1954).

Setae of lacinia 0.8 to 1.0 length of seta of stipes behind lacinia. Prementum without or with less than three accessory setae dorso-laterally. Meshes of microsculpture on all of parietale dorsal surface and latero-ventral surface, on all of discs of nota; alveolae outlined clearly on disc of terga 1 to 8 but undelimited on tergum 9, instead sculpture single-pointed antero-medially on disc, and meshes delimited on sternum of segment 9.

Note about description.- Luff (1976) described very briefly the first and second instar larvae. I did not have access to these, thus I studied a single third instar specimen collected by Lindroth. This specimen was very pale, perhaps a recently molted specimen, thus for color I used descriptions by Lindroth and Luff.

Derivation of specific epithet.- Latin for Lapland, the area of origin of the type.

Distribution.- Specimens of this subspecies occur in the northern boreal regions as far north as the Arctic coast, in the west. The range extends from the northern British Isles to Kamchatka (Lindroth, 1945) and from Alaska to Labrador (for North American distribution see Fig. 157). In North America the species is in the Swan Hills, and Caribou Mountains, Alberta and along the Rocky Mountains as far south as south western Alberta. I studied 80 adults and one third instar larva.

Collecting notes.- Members of this subspecies are very hygrophilous and live where water is very cold. The substrate is of neutral pH, thus there is little or no sphagnum moss but rather one sees mosses of the genus *Paludella* and other short vegetation such as *Marchantia*. The surface is exposed to the sun without or with few small and scattered conifers. This type of habitat is found near springs, brooks, small ponds or on very moist moss without open water. Adults are seen in spring with occurrence sporadic later in summer. Full grown third instar larvae and teneral adults were collected in July in Labrador, thus probably overwintering as adults. They are no doubt good flyers as strongly suggested by two individuals interpreted as stragglers, and collected on the shore of Lesser Slave Lake, Alberta.

Taxonomic notes.- See discussion under *E. l. obliteratus*.

Table 1. Descriptive statistics for *E. lapponicus lapponicus*, based on 10 males and 10 females from mainland northwestern North America (Alaska, Yukon, North West Territories, Alberta, and British Columbia).

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.65-1.97	1.85	0.140	0.043	5.0
PW	1.85-2.22	2.08	0.165	0.049	5.3
EL	4.20-5.10	4.68	0.375	0.113	5.4
HW	1.87-2.15	2.05	0.109	0.320	3.5
B. Proportions					
PL/PW	0.830-0.927	0.886	0.043	0.013	3.2
PL/EL	0.366-0.418	0.395	0.019	0.006	3.1
PL/EW	1.030-1.190	1.110	0.052	0.015	3.1
PL/HW	0.825-0.938	0.902	0.044	0.013	3.2
PW/EL	0.425-0.468	0.446	0.020	0.006	3.1
PW/EW	1.190-1.330	1.260	0.063	0.019	3.3
PW/HW	0.925-1.070	1.020	0.052	0.015	3.4
EL/EW	2.720-3.000	2.820	0.101	0.030	2.4
EL/HW	2.150-2.380	2.290	0.105	0.031	3.1
EW/HW	0.725-0.852	0.810	0.049	0.015	4.0

3.5.2.1.2 Elaphrus lapponicus obliteratus new status

Elaphrus obliteratus Mannerheim 1853: 117. Type locality.- Paul Harbour, Kodiak Island, Alaska; type in Zoological Museum, University, Helsinki; seen by Lindroth 1961: 111. Lindroth 1961: 111.

Adults. Diagnostic combination.- Specimens of this subspecies are recognized by their large size: elytral length (EL) mostly more than 5.5 mm, and by relatively narrower head and shorter pronotum. Means of the following ratios were significantly different from means of E. l. lapponicus samples: PW/HW greater than 1.058, EL/HW more than 2.36, EW/HW more than 0.846 and PL/EL less than 0.386. For details see Table 2.

Adults. Description.- As in E. l. lapponicus except for the ratios mentioned above. Surface features less well impressed than most specimens from other localities in continental North America and Eurasia where pits are impressed and lateral ridges clearly defined in most specimens.

Variation.- See Table 2.

Derivation of specific epithet.- Latin obliteratus = erased, probably in reference to less impressed elytral features.

Distribution.- Known from few localities on Kodiak Island. I examined 23 adults. Larva not known.

Table 2. Descriptive statistics for *E. l. obliteratus*, based on 12 males and eight females from Pinguecula Lake and Bare Lake, both localities on Kodiak Island, Alaska.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	2.00-2.32	2.20	0.121	0.036	3.7
PW	2.40-2.72	2.56	0.125	0.037	3.2
EL	5.15-6.20	5.75	0.359	0.107	4.2
EW	1.90-2.20	2.04	0.133	0.038	4.3
HW	2.25-2.52	2.39	0.105	0.031	2.9
B. Proportions					
PL/PW	0.818-0.880	0.857	0.026	0.008	2.0
PL/EL	0.364-0.395	0.382	0.013	0.004	2.3
PL/EW	1.040-1.130	1.070	0.040	0.012	2.5
PL/HW	0.874-0.968	0.918	0.034	0.010	2.5
PW/EL	0.421-0.471	0.446	0.019	0.006	2.8
PW/EW	1.200-1.320	1.250	0.051	0.015	2.7
PW/HW	1.030-1.130	1.070	0.041	0.012	2.5
EL/EW	2.680-2.950	2.810	0.114	0.034	2.7
EL/HW	2.280-2.550	2.400	0.117	0.035	3.3
EW/HW	0.809-0.903	0.857	0.037	0.011	2.9

United States. ALASKA: Kodiak Island: Bare Lake (5; UASM), Pinguicula Lake (7: UASM), from above two localities (10; MCZC), and one specimen labelled "R. A." = Russian America

Collecting notes.- Lindroth (1969) and Ball reported them abundant in sphagnum bogs.

Taxonomic notes.- Members of many species of ground beetles are larger and even brighter in regions with cool or cold maritime climate (Lindroth, 1955 and 1961). Specimens of this species are larger in these regions (Scandinavia, Anchorage, Labrador and Kodiak). Specimens from Kodiak are much larger than expected. My interest arose when G. E. Ball noted that he collected them on sphagnum moss, a habitat avoided by the mainland beetles with which I am familiar.

Though size is the most striking character as it is taxonomically significantly different from the mainland populations, I studied ratios derived from basic measurements for other evidence of lack of gene flow. Both samples from Scandinavia and western North America differ significantly in their means from those of Kodiak in six ratios of which four are shared. These ratios were tested in relation to body size for correlation. Within each sample there seems to be little or no correlation with size. Between samples for ratios PW/HW and EW/HW there is a correlation but not for ratios PL/EL, EL/HW, PW/EL and PL/PW. Thus mainland specimens differ significantly in their means from the Kodiak sample mean in two ratios PL/EL and

EL/HW. The Scandinavian sample mean is significantly different from the Kodiak sample in ratio PW/EL, and from mainland North American sample mean in ratio PL/PW. Scandinavian and North American sample means differ significantly from each other in ratios PW/EL and PL/PW.

Slight differences between North America and Scandinavia are expected as suggested by differences observed among many other carabid species common to both regions. Despite the great distance, both populations are essentially similar with narrower pronotum in North America. However, differences between North American mainland and Kodiak and Scandinavia suggest lack of gene flow over a long period and that the Kodiak population is evolving independently. Because of habitat differences, significant difference in means of ratios PL/EL and EL/HW, and the unusually larger size I felt justified in ranking the Kodiak population as a subspecies.

Lindroth (1969b: 195-210) in his account of the Kodiak carabid fauna found no evidence of endemic species or races. However, he felt that some carabid species existed on the refugium during at least the last glaciation as suggested by the higher proportion of micropterous species than on nearby Alaska and Kenai Peninsula. A post glacial recolonization would have produced a higher proportion of macropterous individuals. Ball (1969) paid special attention to six micropterous species of Pterostichus in the subgenus Cryobius. He found that three were not different from nearby

Alaska peninsula, while P. parasimilis Ball differed slightly in color, and the means of elytral length for each sex of P. pinguedineus Escholtz and P. riparius Dejean were significantly larger than other coastal Alaskan localities. However, he found no differences in body proportions or in behaviour. Specimens of E. lapponicus obliteratus have diverged to a greater extent as size and means of many proportions are significantly different from the Alaskan and Scandinavian samples, and behavior in the choice of habitat is different. As the beetles are cold hardy, I feel that they survived in the refugium through several glacial periods when selection was probably intensive.

3.5.3 Subgenus Neoelaphrus Hatch

Neoelaphrus Hatch 1951: 113. Type species.- Elaphrus uliginosus Fabricius 1775: 78, designated by Hatch, 1951. Lindroth 1961: 112.

Elaphrus Semenov 1895: 309; not Latreille 1810: 425, who designated the type species as Elaphrus riparius Linnaeus 1758: 407. Lindroth 1961: 112.

Adults. Diagnostic combination.- Mental teeth 0.67 to 0.8 length of mental emargination. Metasternum without setae laterally. Tergum 7 with setae along anterior margin or on entire surface of segment. Elytral pits each with 25 or less punctures (Fig. 132 to 134). Anterior internal row of femur of foreleg with six to 12 setae; tibial fringe (anterior internal row) 0.6 length of tibia and without setae behind fringe. Femur of hind leg with five to 11 setae. Apicoventral surface of basal sclerite of female stylus with numerous spinules (Fig. 73); apex of apical sclerite with one very small seta and, in some members, with second microseta.

Adults. Description.- Color black to brilliant green or copper. Surface in most members brilliant, microsculpture absent or under smooth transparent epicuticular layer.

Head. Medial fovea on frons distinct, in some members with additional smaller foveae posteriorly. Ommatidia of eyes of similar diameter on anterior and posterior surfaces. Clypeus with two setae.

Mouthparts. Grinding edge of right mandible more than 0.5 length of mandible, basal retinacular tooth emarginate, apex of retinacular tooth well anterior to terebral tooth. Maxillary palpomere 3 0.3 to 0.4 length of palpomere 4. Galeomere 1 1.5 length of maxillary palpomere 2. Teeth on internal margin of lacinia alternately small and smaller. Medial teeth of mentum 0.67 to 0.8 depth of mentum emargination. Ligula prominent or moderately so. Submentum with eight major setae and few accessory very small setae.

Thorax. Setae of fringe of anterior and posterior margins of pronotum moderately expanded; fringes not extended to lateral angles; bead of lateral margins not interrupted except near angles in some members; disc with one to five impressions. Suture between proepisternum and proepimeron indistinct. Setae of fringe on anterior margin of prosternum moderately expanded. Postero-lateral ridge of mesosternum absent or indistinct; alveolae of microsculpture on process without or with points, process without setae. Apico-lateral setae of metanotum very small to small. Anterior ridge of metepisternum indistinct. Metasternum without setae laterally.

Abdomen. Tergum 7 with setae along anterior margin or on entire surface. Sternum 4 with 15 or less, and sterna 5 and 6 each with very few (zero to two) or few (12 or less) accessory setae.

Elytra. Striae suggested at base in many members, transverse basal stria distinct at shoulder; mirrors numerous and similar in interval 3. Elytral articulation with four to six distinctly outlined punctures; pits with 25 or less punctures (Fig. 132 to 134); pores in punctures numerous. Setigerous punctures large (40 to 50 microns). Pits without or with two lateral ridges or ridges united (better expressed in pits of interval 3).

Legs. Trochanter of foreleg with one or two setae. Femur with 32 to 57 setae, anterior internal row with six to 12 setae. Surface of tibia with 19 to 25 setae, posterior medial row with seven to 12 setae in both sexes; anterior medial row with six to eight setae; fringe (anterior internal row) 0.6 length of tibia, no other setae posterior to fringe. Tarsomeres 1 to 4 of males with spongy pubescence, tarsomeres 1 to 4 each with four to eight, and tarsomere 5 with two to six accessory setae.

Alveolae of microsculpture on coxa of midleg flat. Trochanter with one or in some individuals with two setae. Femur with 27 to 58 setae; anterior internal row with one to eight setae, external row without or with one to four setae, and posterior external row without or with one seta; alveolae of microsculpture flat. Tibia with 56 to 80 setae. Tarsomeres 1 to 4 each with four to 10 and tarsomere 5 with two to four spinules.

Coxa of hind leg with few setae (one large and two to five medium ones) in inner half of process. Femur with five to 11 setae, anterior external row with one or two setae, anterior internal row without setae; alveolae of microsculpture flat. Tibia with 51 to 80 setae, external row with three to seven setae. Tarsomeres 1 to 4 each with four to 12 and tarsomere 5 with two to 10 spinules.

Male genitalia. Postero-dorsal surface of internal sac with large scales.

Ovipositor. Apico-ventral surface of basal sclerite of stylus with numerous spinules, apical sclerite with few stout spines along ridge, apex of sclerite with one very small seta or in some members with one more extremely small seta (Fig. 73).

First Instar Larvae. _Diagnostic combination_.- Nasale very prominent, nasale teeth separated by small median projection, teeth large (Fig. 90b). Epicranial suture subequal or longer than scape, and head elongate (Fig. 90a); lateral convexity in front of neck longer than one behind neck; triangle formed by setae DEP, VEP-P and VEM-P equilateral. External side of stipes thickly sclerotized; setae on dorsal internal surface with about 30 setae, those in apical 0.3 approximating one row; posterior ventral pores distant, internal one well ahead of posterior one. Maxillary palpomere 1 1.2 to 1.5 length of palpomere 2.

First Instar Larvae. Description.- Head mostly pale to mostly darker except at base, and nota and terga 1 to 9 brown.

Head. Nasale very prominent, teeth separated by small medial projection, teeth large (Fig. 90b); pore MMP-E internal to egg-burster anterior end, pore MA-I in front of seta MMA. Epicranial suture subequal to or longer than antennal scape, head elongate: lateral convexity in front of neck longer than convexity posterior to neck (Fig. 90a); seta DI-A posterior to postero-lateral angle of frontale, angle formed by seta DI-A and pores DI-P and DMP-E open (about 110 to 130°), system DMM in posterior position with seta DMM-P level with postero-lateral angle of frontale, triangle formed by setae DEP, VEP-P and VEM-P equilateral.

Head proportions as follows: PW/PML 1.2 to 1.4, PW/PLP 1.6 to 2.1, PML/PBW 0.9 to 1.1, FW/OL 2.3 to 5.1, PL/OL 3.0 to 4.0, Pl/OL 2.4 to 4.0, Pl/PL 1.4 to 2.3, and Pl/OL 4.4 to 5.0.

Mouthparts. Stipes three or four times longer than wide; external surface thickly sclerotized; setae on dorso-internal surface 0.5 with about 30 setae, setae in apical third roughly in one row; posterior ventral pores distant: internal one well ahead of external one. Maxillary palpomere 1 1.2 to 1.5 length of palpomere 2. Seta on galeomere 1 very small to small; microseta on internal side of galeomere 2 in apical 0.2 to 0.6. Seta of lacinia 0.5 to 0.67 length of seta behind lacinia. Prementum with small antero-lateral spinule on dorsal side.

Thorax. Sculpture absent from disc of pronotum. Proepisternal seta small to medium-small. Mesonotal setae AIM and AIE-I medium-large to large, setae PIM-I and PIE-A very large, and seta PII-P medium-small; alveolae of microsculpture on 10 to 50% of disc surface, pointed sculpture absent from posterior band or, in one member, barely suggested on 60% of band surface. Mesepipleural seta medium-small. Mesosternal seta medium.

Membrane laterally with 15 to 75%, and ventrally with 15 to 45% of surface with pointed sculpture.

Abdomen. Seta AII and AIM on terga 1 to 8 medium-small to medium; pointed sculpture on terga 1 to 8 absent or, in one member, on 5% of surface, sculpture on urogomphus of tergum 9 on surface single-pointed. Seta on epipleuron of segments 1 to 5 medium to large, and of segment 9 medium-small. Sternal seta of segments 2 to 7 medium-small to medium. Internal seta of internal poststernite of segments 1 to 8 very small. Pointed sculpture on membrane restricted dorsally to baso-lateral area of terga and ventrally absent between sternites of segments 2 to 7.

Second Instar Larvae. Diagnostic combination.- Pronotal epipleuron with 20 to 35 accessory pores. Mesonotum without sculpture on anterior band. Basic seta AM-P of tergum 10 medium-large to large. Discs of terga 1 to 8 each with 16 to 36 accessory setae. Major accessory seta at base of urogomphus of tergum 9 postero-lateral in position, seta large. Hypopleuron of segments 1 to 8 each with eight to 20 accessory setae.

Second Instar Larvae. Description.- Head and body nota and terga colored as first instar but in many members color pattern at base of urogomphus distinct.

Head. Basic seta MP on frontale extremely small to very small.

Mouthparts. Dorsal antero-lateral basic spinule small.

Thorax. Pronotal epipleuron with two to seven accessory setae and five to eight accessory pores; major accessory setae medium-small to medium; alveolae of microsculpture absent from disc of pronotum. Mesonotum with 15 accessory setae; major accessory setae on row behind posterior row of basic setae medium size; pointed sculpture absent laterally or up to 15% of disc surface, anterior band with pointed sculpture. Mesepimeron with two to 13 accessory setae; sculpture absent. Metathorax as mesothorax.

Abdomen. Seta MPP-E on urogomphus of tergum 9 very small, seta AII and AIM of terga 1 to 8 medium to large, and seta AM-P of tergum 10 medium-large to very large; disc of terga 1 to 8 each with 16 to 36 accessory setae, and of tergum 10 with one to four accessory setae; basal major accessory setae on urogomphus postero-lateral in position, seta large; sculpture of disc of terga 2 to 8 single-pointed, on urogomphus of tergum 9 barely suggested or scale-like (broad single-points), sculpture absent from anterior band of terga 1 to 8, pointed sculpture of anterior band of tergum 9 absent or on 10% of band surface, sculpture absent or on 5% of posterior band surface, sculpture restricted on disc of tergum 1 or 3 or sculpture restricted on all terga. Hypopleuron of segments 1 to 8 each with eight to 20 accessory setae; minor accessory setae medium-small. Sternite of segments 2 to 7 each with 12 to 18, of segment 8 with 12 to 22, of segment 9 without or with 2 accessory setae, and of segment 10 with three major accessory setae; sculpture on segments 2 to 7 multi-pointed. External poststernite of segment 1 with two to four, and of segments 2 to 7 each with four to seven accessory setae. Internal poststernite of segment 1 with two, and of segments 2 to 7 each with three to four accessory setae.

Membrane pointed sculpture restricted baso-laterally on dorsum of abdomen: along lateral and posterior margin of terga.

Third Instar Larvae. Diagnostic combination.- Meshes of microsculpture on dorsal surface of parietale restricted to lateral edge. Proepisternum with 25 accessory setae. Proepimeron with 25 accessory pores. Meshes of microsculpture on discs of mesonotum and metanotum absent or up to 90% of disc surface. Mesepimeron with 20 accessory setae. Basic seta on anterior sternite medium-small. Basic seta PI-P of tergum 10 large; sculpture on anterior band of terga 1 to 8 absent or up to 10% of band surface. Epipleuron of segments 2 to 8 each with 17 to 60 accessory setae, sculpture absent from segment 1. Hypopleuron of segments 1 to 8 each with 14 to 47 accessory setae; major accessory setae very large.

Third Instar Larvae. Description.- Head dorsally mostly pale to pale only at base. Nota and terga 1 to 8 black or brown, base of urogomphus of tergum 9 dark or pale.

Head. Meshes of microsculpture on dorsal surface of parietale restricted to lateral edge.

Mouthparts. Prementum with about six accessory setae dorso-laterally, and with one accessory seta antero-laterally; latero-basal accessory setae medium-small.

Thorax. Disc of pronotum without or with alveolae of microsculpture up to 75% of surface. Proepisternum with 25 accessory setae. Proepimeron with 25 accessory pores. Mesonotal epipleuron with one or nine accessory setae; major accessory setae medium-large to large; alveolae of microsculpture absent or on up to 90% of surface of disc.

Mesepipleural major accessory seta medium-small to medium. Mesepimeron with 20 accessory pores; major accessory setae medium-small. Basic seta of anterior sternite medium-small. Metathorax as mesothorax except: anterior pleurite with two to seven accessory pores; major accessory seta medium-small.

Abdomen. Major knobs of urogomphus of tergum 9 in lateral view medium or large (Fig. 98c), and in dorsal view small or large; basic seta PI-P on tergum 10 large; disc of terga 1 to 8 each with 35 to 140 accessory setae; pointed sculpture on anterior band of terga 1 to 8 absent or up to 10% of band surface, and of tergum 9 absent or on 20% or 60% of band surface; alveolae of microsculpture restricted on disc of tergum 1 or 5 or very restricted on all terga. Epipleuron of segments 2 to 8 each with 17 to 60 accessory setae; sculpture absent from segment 1. Hypopleuron of segments 1 to 8 each with 14 to 47 accessory setae; major accessory setae very large. Sternite of segment 1 with four to 12 accessory setae, of segments 2 to 7 each with 18 to 24, of segment 8 with 18 to 38, of segment 9 with two to eight, and of segment 10 with six to 12 minor accessory setae; size of major accessory setae of segments 2 to 7 medium-small to medium. External poststernite of segment 1 with five to 15, and of segments 2 to 7 each with nine to 18 accessory setae. Internal basic seta of internal poststernite very small or medium; segment 1 with one to five, and segments 2 to 7 each with three to seven accessory setae.

Distribution.- Members of this subgenus occur across the northern hemisphere from subarctic regions to the northern half of the warm temperate zone (central France; Honshu Island, Japan; California, Washington, D.C.).

Taxonomic notes.- The members of this subgenus are arranged in three groups: the *uliginosus* group, the *fuliginosus* group and the *cupreus* group. Each group is characterized in the key as well as in the text. My main reason for recognizing these three monophyletic groups was for zoogeographic reasons. Basically, the *uliginosus* group evolved in Eurasia, the *fuliginosus* group is restricted to eastern North America and the *cupreus* group has two lineages of which one is Euroasiatic and the other North American.

3.5.3.1 Key to the species of subgenus *Neoelaphrus* Hatch

Adults

1. Fringe of setae along posterior margin of pronotum terminated near postero-lateral angle (40 to 120 microns) (Fig. 17a). Lateral margin of pronotum in lateral view sinuate near middle, pronotal epipleuron narrowest at this point (Fig. 17b). Bead of pronotal lateral margin wide (20 to 30 microns. Pronotum with one antero-submedial impression (indistinct in individuals of *E. splendidus*). Specimen from Eurasia. 2

1'. Fringe of setae along posterior margin of pronotum terminated away (150 to 250 microns) from postero-lateral angles (Fig. 18a and 19). Lateral margin of pronotum in lateral view not sinuate near middle, pronotal epipleuron equally narrow from middle to anterior margin (Fig. 18b). Bead of pronotal lateral margin absent, narrow (10 to 15 microns), or in one North American member wide. Pronotum without antero-submedial impression. 6

2.(1). Elytron with four rows of very distinctly outlined subconvex mirrors on intervals 3, 5, 7 and 9. Upper surface including elytral pits brilliant golden green metallic. Pronotum with two discal impressions on each side. Punctures on elytral intervals 4, 6 and 8 large (30 to 40 microns in size), finer on head and pronotum (20 to 25 microns). Specimen from eastern Siberia. ....E. splendidus Fisher von Waldheim p.179

2'. Elytron with one or two rows of distinctly outlined flat mirrors on intervals 3 or 3 and 5. Upper surface of most members not brilliant green; elytral pits purple or if green, then surface brown-copper. Punctures of head, pronotum and intervals 4, 6 and 8 small (20 to 25 microns). 3

3.(2'). Punctures on intervals 4, 6 and 8 scattered (100

to 150 microns apart). Lateral ridges of elytral pits very prominent and wide (Fig. 132). Specimen from northern Honshu Island, Japan.
..........................*E*. *japonicus* Ueno p.181

3'. Punctures in intervals 4, 6 and 8 denser (30 to 40 microns apart). Lateral ridges of elytral pits not prominent, narrow or absent (Fig. 119 and 120). 4

4.(3'). Dorsal surface bright brown copper and pits metallic green. Elytra elongate. Specimen from the Chinese province of Kansu.
........................*E*. *potanini* Semenov p.192

4'. Dorsal surface dark or brilliant green or copper, or brilliant brown-copper in few specimens; elytral pits purple. Elytra shorter (El/EW ranges from 2.53 to 3.00 with averages of 2.70 and 2.72). 5

5.(4'). Dorsal surface dark green or copper (some individuals brilliant. Intervals 4, 6 and 8 subcostate (except specimens from central Asia). Meshes of microsculpture on surface and alveolae flat (Fig. 137). Elytral pits slightly impressed or not; lateral ridges moderately narrow or absent (most specimens from central Asia) (Fig. 119). Specimen from Europe as far south as central France. ....*E*. *uliginosus* Fabricius p.183

5'. Dorsal surface brilliant green-olive or brown-copper. Meshes of microsculpture absent from surface except near shoulder, elytral pits and postero-lateral impressions of pronotum (Fig. 138). Elytral pits deeply impressed (Fig. 120); intervals 4, 6 and 8 not costate; lateral ridges of pits very narrow or absent. Specimen from southern Spain to the Pyrenees.

......E. pyrenaeus Fairmaire and Laboulbène p. 189

6. (1'). Lateral margin of pronotum in vertical plane rounded or beaded. Bead wide (20 to 30 microns). Punctures on pleura and laterally on abdominal sterna large (30 tc 45 microns); punctures apparently larger (about 80 microns) because of widely depressed area around each puncture--best seen on proepisternum (Fig. 107). Abdominal sterna 5 and 6 each without or with one or two accessory setae medially (Fig. 139). Tibia of foreleg of male with sharp and large projection at base of posterior spur and with very small projection at base of apical spur--best seen in posterior view (Fig. 149). Specimen from eastern North America. 7

6'. Lateral margin of pronotum in vertical plane beaded. Bead narrow (10 to 15 microns wide). Punctures on pleura and laterally on abdominal sterna smaller (20 to 35 microns), and area around each puncture narrowly or not depressed

(Fig. 108). Abdominal sterna 5 and 6 each with five to 15 accessory setae or without accessory setae and punctures on ventral surface very dense (20 to 25 microns). Tibia of foreleg of male without projection at base of both spurs (cuticle at base of posterior spur in some members sharp but not projected). Specimen from Eurasia or North America. 9

7.(6). Dorsal surface dark green. Pronotal lateral margin beaded along entire length; bead 20 to 30 microns wide. Dorsal surface of tibia and tarsomeres green metallic. Abdominal sternum 7 of males with 10 to 20 accessory setae. ....*E. fuliginosus* Say p.195

7'. Dorsal surface with very dark copper hue or surface brass silver. Lateral margin of pronotum in vertical plane rounded or barely angulate near middle; bead absent (Fig. 107). Dorsal surface of tibia and tarsomeres purple metallic. Abdominal sternum 7 of male without accessory setae (Fig. 139). 8

8.(7'). Dorsal surface nearly black with copper hue; antennomeres 1 to 3 black. Lateral ridges of elytral pits very convex and wide (Fig. 132). Elytron with two rows of well outlined mirrors on intervals 3 and 5; mirrors little contrasted against dark background color of intervals 4, 6 and 8. Trochanter of foreleg with one seta (Fig. 145). Punctures irregularly scattered dorsally (10 to 200 microns apart).

....................E. cicatricosus LeConte p.202

8'. Dorsal surface color brass-silver; antennomeres 1 to 3 reddish brown. Lateral ridges of elytral pits very narrow or absent (Fig. 121). Elytron with one row of indistinctly outlined but contrasted mirrors on interval 3. Trochanter of foreleg with two setae. Punctures rather uniformly distributed on dorsal surface (10 to 30 microns apart on head and elytral intervals 4, 6 and 8 and 20 to 40 microns on pronotum) (Fig. 121 and 104). ....E. lindrothi new species p.209

9. (6'). Lateral ridges of elytral pits not fused anteriorly or posteriorly; ridges wide (Fig. 132). One or two rows of mirrors distinctly outlined and contrasted against duller intervals 4, 6 and 8. Alveolae of microsculpture flat or subconvex on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 132). Specimen from Eurasia. .10

9'. Lateral ridges of elytral pits distinctly fused anteriorly and posteriorly or indistinctly so (then ridges narrow) (Fig. 133 and 134). Elytron with one or two rows of distinctly outlined but slightly contrasted mirrors against brilliant intervals 4, 6 and 8. Meshes of microsculpture absent or suggested in spots on head, pronotum and intervals 4, 6 and 8 (in some individuals of one species, meshes outlined on intervals but meshes under a thin very smooth and transparent layer, thus meshes not impressed at surface of layer) (Fig. 133 and 134). Specimen from North America. 11

10.(9). Dorsal surface dark green except near head and pronotal impression where brilliant green; dorsal surface of tibia and tarsomeres green metallic. First sutural pit of elytron with eight to 12 punctures. Punctures of dorsal surface denser: on elytral intervals 4, 6 and 8 punctures 25 to 40 microns apart. Internal 0.33 of hind coxa with eight to 15 accessory setae. Specimen from boreal Sibiria. ....E. sibiricus Motschulsky p.215

10'. Dorsal surface dark bronze-copper; dorsal surface of tibia and tarsomeres purple metallic. First sutural pit of elytron with 15 to 25 puctures. Punctures of dorsal surface scattered: on elytral intervals 4, 6 and 8 punctures 20 to 100 microns apart. Internal 0.33 of hind coxa with three to seven accessory setae. Specimen from cold temperate or boreal Eurasia.

......................E. cupreus Duftschmid p.219

11.(9'). Punctures moderately scattered (10 to 100 microns apart) on pleura and laterally on abdominal sterna. Prosternal intercoxal process of about 50% of specimens with one to four accessory setae. Tibia of midleg of male with sharp apico-internal projection between spurs (Fig. 150). Punctures on elytral intervals 4, 6 and 8 scattered (30 to 120 microns apart) (Fig. 122). ....E. clairvillei Kirby p.227

11'. Punctures very dense (10 to 20 microns apart) on pleura, and laterally on basal abdominal sterna. Prosternal intercoxal process without accessory setae. Tibia of midleg of male without projection between spurs. Punctures on elytral intervals 4, 6 and 8 much denser (10 to 20 microns apart) or much more scattered (more than 200 microns apart). 12

12.(11'). Dorsal surface olive, blue-green, dark brown-olive, or red-brown; dorsal surface of tibia and tarsomeres green or copper metallic; antennomeres 1 to 3 brown. Pronotum with two discal impressions. Lateral ridges of elytral pits very narrow (Fig. 134); first sutural pits clearly outlined. Dorsal punctures dense (15 to 20 microns) on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123). Abdominal sterna 5, 6 and 7 each without or with less than two accessory setae. Specimen from Rocky Mountains, northern

United States or adjacent Canada.
.......................*E*. olivaceus LeConte p.249

12'. Dorsal surface brilliant black; dorsal surface of tibia and tarsomeres purple metallic; antennomeres 1 to 3 black. Pronotum with one discal impression. Lateral ridges of elytral pits wide and convex (Fig. 133); elytral pits with four to five punctures; setigerous punctures in pits very indistinctly outlined. Dorsal punctures on head about 60 microns apart, on pronotum 10 to 200 microns apart and on elytra 200 microns or more apart. Abdominal sterna 5, 6 and 7 with five to 20 accessory setae. Specimen from California or westernmost Nevada.
.......................*E*. laevigatus LeConte p.263

First Instar Larvae

1. Dorsal surface of parietale pale except near frontale and antennae. Setae AII and AIE-I of mesonotum and metantoum large. Meshes of microsculpture barely distinct dorso-laterally on parietale. Pointed sculpture near suture of mesonotum and metanotum absent or on 2% or less of disc. Specimen from east of the North American prairies. 2

1'. Dorsal surface mostly dark except laterally.

Setae AII and AIE-I of mesonotum and metanotum medium-large. Meshes of microsculpture distinct dorso-laterally on parietale. Pointed sculpture on 10% of disc of mesonotum and metanotum near suture. Specimen from North America or Eurasia. 3

2. (1). Teeth on nasale. Pointed sculpture on 5% of ventro-lateral surface of parietale. Darker pattern on dorsal surface of parietale extended to occipital suture. Pointed sculpture on entire surface of abdominal sternite 10.
........................E. fuliginosus Say p.195

2'. Teeth absent from nasale. Pointed sculpture absent from ventro-lateral surface of parietale. Darker pattern on dorsal surface of parietale not extended to occipital suture. Pointed sculpture absent from abdominal sternite 10.
....................E. cicatricosus LeConte p.202

3.(1'). Meshes of microsculpture absent from disc of pronotum. Pointed sculpture on ventral surface of membrane of prothorax not extended toward episternum. 4

3'. Meshes of microsculpture on 5% or more of disc of pronotum. Pointed sculpture on ventral surface of membrane of prothorax restricted medially. 5

4.(3). Meshes of microsculpture restricted dorso-laterally on parietale to 7% of surface; pointed sculpture extended laterally on 5% of dorsal and ventral surface of parietale. Specimen from Eurasia. ....*E. cupreus* Duftschmid p.219

4'. Meshes of microsculpture more extended laterally to 20% of dorsal surface of parietale; pointed scultpure extended laterally on 10% of dorsal surface of parietale and 2% of ventral surface. Specimen from North America.
......................*E. clairvillei* Kirby p.227

5.(3'). Meshes of microsculpture more restricted: pointed meshes on 5% of dorsal surface of parietale and 3% of ventral surface. Seta AII-E of pronotum medium. Pointed sculpture on mesonotum and metanotum on 20% of surface of disc near suture but only 5% of disc laterally, and absent from posterior band. Specimen from Rocky Mountains, northern United States or adjacent Canada.
......................*E. olivaceus* LeConte p.249

5'. Meshes of microsculpture extended laterally on 50% of dorsal surface of parietale and 15% of ventral surface. Seta AII-E of pronotum large. Pointed sculpture on mesonotum and metanotum less expanded near suture (10% of disc) and on 35% of disc laterally, and on 60% of posterior band. Specimen from California and westernmost Nevada.
......................*E. leavigatus* LeConte p.263

Second Instar Larvae

1. Dorsal surface of parietale dark near frontale and base of antennae. Setae AII and AIE-I of mesonotum and metanotum large. Epicranial suture shorter: 0.6 to 0.8 length of antennal scape. Pointed sculpture absent from dorso-lateral surface of parietale. Seta AM-P of tergum 10 very large. Specimen from eastern North America. 2

1'. Dorsal surface of parietale mostly dark. Seta AII and AIE-I of mesonotum and metanotum medium-large. Epicranial suture as long as antennal scape. Pointed sculpture laterally on 15% or more of dorsal surface of parietale. Seta AM-P of tergum 10 large or smaller. Specimen from Eurasia or North America. 3

2.(1). Sclerite typically setose: pronotal epipleuron with one or two accessory setae, urogomphus of tergum 9 with about seven accessory setae (Fig. 98b). Meshes of microsculpture clearly outlined on nota, terga and urogomphi.
........................*E. fuliginosus* Say p.195

2'. Sclerites markedly setose: pronotal epipleuron with seven accessory setae, urogomphus of tergum 9 with about 25 accessory setae (Fig. 99a). Meshes of microsculpture absent from nota, very restricted on terga, and suggested on urogomphus.
.....................*E. cicatricosus* LeConte p.202

3.(1'). Pointed sculpture near suture on 2% of disc of mesonotum and 10% of disc of metanotum, laterally on 15% of disc of both nota, and on 10% of anterior band of tergum 9. 4

3'. Pointed sculpture absent from suture area of mesonotum and metanotum, absent laterally or present on 10% of disc surface of both nota, and absent from anterior band of tergum 9. 5

4.(3). Pointed sculpture of membrane on ventral surface of abdomen not extended toward sternites 2 to 7. Meshes of microsculpture indistinctly outlined on 50% of disc of pronotum. Specimen from Eurasia. ....E. cupreus Duftschmid p.219

4'. Pointed sculpture of membrane on ventral surface of abdomen extended toward sternites 2 to 7. Meshes of microsculpture clearly outlined on 10% of disc of pronotum. Specimen from North America. ....E. clairvillei Kirby p.227

5.(3'). Pointed sculpture laterally on 15% of dorsal surface of parietale and 3% of ventral surface. Meshes of microsculpture on 30% of disc of pronotum, and 40% of disc of mesonotum and metanotum. Pointed sculpture absent laterally from nota. Specimen from Rocky Mountains, northern United States or adjacent Canada. ....E. olivaceus LeConte p.249

5'. Pointed sculpture laterally on 30% of dorsal surface of parietale and 10% of ventral surface.

Meshes of microsculpture on 75% of disc of pronotum, and 90 to 100% of disc of mesonotum and metanotum. Pointed sculpture laterally on 10% of disc of mesonotum and metanotum. Specimen from California or westernmost Nevada.
......................*E. laevigatus* LeConte p.263

Third Instar Larvae

1. Dorsal surface of parietale dark only near frontale and antennal base. Epicranial suture shorter: 0.6 to 0.8 length of antennal scape. Pointed sculpture absent from dorso-lateral surface of parietale. No sculpture on urogomphus of tergum 9. Abdominal sternites 2 to 7 with about 24 or more accessory setae. Specimen from east of North American prairies. 2

1'. Dorsal surface of parietale mostly dark except laterally. Epicranial suture subequal to antennal scape. Pointed sculpture laterally on 15% or more of dorsal surface of parietale, and on urogomphus of tergum 9. Abdominal sternites 2 to 7 each with about 18 accessory setae. Specimen from North America or Eurasia. 3

2.(1). Sclerites less setose: posterior band of mesonotum and metanotum without accessory setae, urogomphus of tergum 9 with about seven accessory setae (Fig. 98c). Meshes of microsculpture clearly outlined over most of nota and terga.

........................*E. fuliginosus* Say p.195

2'. Sclerites markedly setose: posterior band of mesonotum and metanotum with five to 15 accessory setae laterally, urogomphus with about 30 accessory setae (Fig. 99b). Meshes of microsculpture absent from nota and membrane, very restricted on terga.

.....................*E. cicatricosus* LeConte p.202

3.(1'). Meshes of microsculpture absent from disc of pronotum. Pointed sculpture laterally on 10% of disc of mesonotum and metanotum, and on 60% of anterior band of tergum 9. Abdominal sternite 9 with about six accessory setae. Pointed sculpture on 5% of more of posterior band of terga 1 to 8.

....4

3'. Meshes of microsculpture on 10% or more of disc of pronotum. Pointed sculpture absent from mesonotum and metanotum, and from anterior band of tergum 9. Abdominal sternite with two accessory setae. Pointed sculpture absent from posterior band of terga 1 to 8. Specimen from North America. 5

4.(3). Pointed sculpture absent from suture area of disc of mesonotum and on 3% of disc of metanotum. Terga 1 to 5 partly or mostly without pointed

sculpture on disc. Specimen from Eurasia.
......................._E_. _cupreus_ Duftschmid p.219

4'. Pointed sculpture near suture on 10% of disc of mesonotum and metantoum. Only terga 1 and 2 partly or mostly without pointed sculpture on disc. Specimen from North America.
........................_E_. _clairvillei_ Kirby p.227

5.(4'). Meshes of microsculpture on 10% of disc of pronotum, and 40% of disc of mesonotum and metanotum. Pointed sculpture absent from anterior band of terga 1 tc 8. Specimen from Rocky Mountains, northern United States or adjacent Canada. ...._E_. _olivaceus_ LeConte p.249

5'. Meshes of microsculpture on 75% of disc of pronotum, and on 90 to 100% of disc of mesonotum and metanotum. Pointed sculpture on 5% or more of anterior band of terga 1 to 8. Specimen from California or westernmost Nevada.
......................_E_. _laevigatus_ LeConte p.263

The _uliginosus_ group

Diagnostic combination.- This group is recognized as follows: setae of fringe along posterior margin of pronotum not extended to postero-lateral angle, terminated near middle of postero-lateral impression or slightly nearer angle (Fig. 17a); pronotum very wide, in lateral view lateral margin depressed, pronotal epipleuron narrower near middle (Fig. 17b). Upper surface with more impressions; anterior transverse impression very short and deeply impressed; disc with antero-submedial deep impression extended anteriorly (also in most members with similar impression submedially extended from short deeply impressed posterior transverse impression), and with two small impressions antero-lateral to main discal impression. Hind coxae with punctures externally on process and laterally on coxa.

3.5.3.2 Elaphrus splendidus Fischer von Waldheim

Elaphrus splendidus Fischer von Waldheim 1828: 267. Reported from Mongolia. Dejean 1831: 587.

Adults. Diagnostic combination.- Adults of this species are easily recognized by the very brilliant green dorsal surface and by four rows of very sharply outlined mirrors on the elytra. Otherwise they are very similar to adult E. uliginosus in external features. The apex of the median lobe is characteristic: apex not twisted and sharp (30 microns in width) in dorsal view, in lateral view as in E. uliginosus but relatively wider.

Adults. Description.- dorsal surface (including pits) very brilliant green metallic except for brilliant black mirrors, ventral surface dark golden green metallic, appendages black except femur with green metallic hue. Head relatively wider than thorax: EL/HW greater than 2.24. Pronotum without small impressions antero-lateral to main discal impressions. Pits shallowly impressed, lateral ridges narrowly outlined or absent; mirrors clearly outlined on intervals 3, 5, 7 and 9.

Integument scultpure. Punctures of elytral intervals 4, 6 and 8 large (30 to 40 microns in size), finer on pronotum and head (20 to 25 microns in size), and large ventrally (30 to 40 microns in size). Distribution of punctures similar to _E_. _uliginosus_; puncture density as _E_. _uliginosus_ but denser on intervals 4, 6 and 8.

Alveolae of microsculpture absent from intervals 4, 6 and 8 or indistinctly outlined, absent on pronotum or present in areas.

Male genitalia.- Median lobe in dorsal view not twisted and apex sharp (30 microns in width) (Fig. 41a), in lateral view spatula very slightly enlarged as in _E_. _uliginosus_ but spatula relatively wider (Fig. 41b).

Measurements _and_ _proportions_.- Based on four specimens from Omsulcschan in northeastern Siberia. PL, 1.8-1.94-2.0 mm; PW, 2.1-2.33-2.4 mm; EL, 4.6-4.98-5.1 mm; EW, 1.7-1.80-1.9 mm; HW, 2.0-2.11-2.2 mm; PL/PW 0.816-0.834-0.854; PL/EL, 0.385-0.389-0.398; PL/EW, 1.05-1.08-1.12; PL/HW, 0.867-0.920-1.000; PW/EL, 0.462-0.467-0.476; PW/EW, 1.28-1.29-1.32; PW/HW, 1.04-1.10-1.17; EL/EW, 2.71-2.77-2.82; EL/HW, 2.24-2.36-2.51; EW/HW, 0.807-0.852-0.890.

Variation.- I have seen only four specimens so the variation is expressed above.

Derivation of specific epithet.- From latin meaning magnificent.

Distribution.- Known from Mongolia and Eastern Siberia to Kamchatka. I have seen four specimens from Omsulcschan USSR, and dissected the only male.

Geographical affinities.- The range of this species is isolated from any other members of the *uliginosus* group. However, it is sympatric with *e. sibiricus* and perhaps with *E. cupreus*.

Relationships.- It is the sister group of *E. uliginosus*. This species is also close to the conservative *E. japonicus*. However, the relationships of this last species remain obscure.

3.5.3.3 *Elaphrus japonicus* Ueno

Elaphrus japonicus Ueno 1954: 718. Type locality.- 'Takinomata, Takedate, Aomori Prefecture, Japan.' Nakane 1973: 4.

Adults. Diagnostic combination.- Adults of this species are easily recognized by the very scattered punctation dorsally especially in intervals 4, 6 and 8 where punctures are about 100 to 150 microns apart. The upper surface is very dark brown copper (as E. cupreus) and tibiae mostly piceus. Mirrors in intervals 3 and 5 well outlined though contrasting only slightly. Apex of median lobe of males in dorsal view not twisted and narrow (30 microns in width) (Fig. 42a), in lateral view spatula enlarged ventrally (Fig. 42b).

Adults. Description.- Very dark brown copper dorsally except for purple pits, ventrally black with metallic golden hue, tibiae piceous, and tarsomeres dark blue dorsally. Pronotum impressions numerous as in E. uliginosus. Pits of elytra deeply impressed, lateral ridges large and prominent.

Integument sculpture. Punctures fine on dorsal surface (20 to 25 microns in size), and ventrally larger (30 to 40 microns). Punctures on dorsal surface scattered: on intervals 4, 6 and 8 punctures 100 to 150 microns apart.

Alveolae of microsculpture flat, lines absent from mirrors.

Male genitalia.- Apex of median lobe in dorsal view (Fig. 42a) not twisted and narrow (30 microns in width), in lateral view spatula enlarged ventrally (Fig. 42b).

Measurements and proportions.- Based on two specimens from Aomori Pref., Japan. PL, 1.8-1.9 mm; PW, 2.1-2.3 mm; EL, 4.6-4.9 mm; EW, 1.7-1.8 mm; HW, 2.2-2.3 mm; PL/PW, 0.835-0.847; PL/EL. 0.388-0.391; PL/EW, 1.04-1.07; PL/HW, 0.828-0.835; PW/EL, 0.462-0.464; PW/EW, 1.25-1.27; PW/HW, 0.977-1.000; EL/EW, 2.68-2.75; EL/HW, 2.11-2.15; EW/HW, 0.770-0.802.

Distribution.- Known from northern and central Honshu Island, Japan. I have seen specimens from Takedate-mura, Aomari Pref. (UASM, HGou). I dissected two males and saw the illustration of a third one in Nakane (1973).

Geographical affinities.- The only known representative of the *uliginosus* group in Japan. It is parapatric with the lowland *E. sibiricus*.

Relationships.- The relationships of this conservative member of the *uliginosus* group are not clarified yet.

3.5.3.4 *Elaphrus uliginosus* Fabricius

Elaphrus uliginosus Fabricius 1792: 178. *Type locality*.- Germany. Jeannel 1941: 218.

Elaphrus latithorax Schönherr 1826. *Nomen nudum*. Dejean 1826: 269.

Elaphrus impressifrons Chaudoir 1842: 815.

Elaphrus italicus Del Torre 1877: 23. Known from Italy. Schilsky 1889: 194.

Elaphrus uliginosus purkynei Obenberger 1917: 9. *Type locality*.- Cepelare, Bulgaria. Louvet 1925: 20.

Elaphrus uliginosus laevisculptus Bänninger 1917: 147. *Type locality*.- Tien-shan. Louvet 1925: 20.

Elaphrus bedeli Méquigon 1924: 127. *Type locality*.- Scalas, France. Louvet 1925: 20.

Elaphrus viridicupreus Louvet 1925: 18. *Type locality*.- Sedan France.

Adults. Diagnostic combination.- Adults distinguished from those of E. pyrenaeus, its closest relative, as follows: most specimens dark green or copper dorsally; punctures on proepisternum less dense (punctures generally 35 microns apart); intervals 4, 6 and 8 with clearly outlined alveolae of microsculpture (Fig. 137), and subcostate; mirrors more sharply outlined at least on interval 3; pits moderately impressed, lateral ridges generally distinct (Fig. 119). Distinguished from remaining species of the group by characters in the key.

Adults. Description.- Dorsal surface dark green or copper, rarely brilliant green; ventral surface with dark green or blue metallic reflections; legs very dark purple except dark golden green femur; and elytral pits in most specimens clearly blue metallic.

Head. In most specimens wider than thorax. Pronotum with postero-submedial impression in most specimens, and with two small impressions antero-lateral to main discal impression. Pits slightly or not impressed, lateral ridges in most specimens clearly outlined except for specimens from western Himalaya; mirrors in interval 3 sharply outlined and flat, in intervals 7 and 9 mirrors indistinctly outlined; intervals 4, 6 and 8 in most specimens subcostate. Abdominal sterna 5, 6 and 7 each with two to 15 accessory setae.

Integument sculpture. Punctures on head, pronotum and elytral intervals fine (20 to 25 microns in size), and large along ventral surface on thoracic pleura and laterally on abdominal sterna (30 to 40 microns in size). Punctures moderately dense on elytral intervals 4, 6 and 8 (30 to 40 microns apart), and on thoracic pleura; proepisternum punctures 30 to 40 microns apart on disc of most specimens.

Alveolae of microsculpture well outlined and flat on dorsal surface except on mirrors, alveolae convex in pits and postero-lateral angles of pronotum.

Male genitalia.- Apical portion of median lobe very twisted in dorsal view and thickness of spatula at apex 65 microns (Fig. 43a); in lateral view spatula slightly enlarged subapically, narrower at base of spatula (Fig. 43b).

Measurements _and_ _proportions_.- See Tables 3 and 4.

Variation.- Specimens from central Europe, Ural Mountains in USSR and Tien-shan Mountains (USSR and China) do not differ significantly in means of measurements and proportions. However specimens from Tien-shan Mountains seem smoother as pits are only slightly impressed, and lateral ridges of pits are indistinctly outlined. This difference is similar to a clinal change observed for _Elaphrus_ _clairvillei_ where specimens appear smoother in mountains of Colorado and Arizona. Thus, I assume there is gene flow or that gene flow was interrupted recently. However the Italian sample differs significantly in the means of EL/HW and PW/HW and in its smaller size (EL,EW,PL and PW) from the above three samples. I feel this mountain form is not connected by gene flow to the main French population. However, my sample is too

Table 3. Descriptive statistics for *E. uliginosus* based on 10 males and 10 females from central France and Switzerland.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.4	2.08	0.185	0.054	5.8
PW	2.2-2.6	2.41	0.205	0.061	5.7
EL	4.7-5.5	5.10	0.381	0.114	5.0
EW	1.7-2.1	1.87	0.167	0.050	5.9
HW	2.2-2.6	2.33	0.164	0.049	4.7
B. Proportions.					
PL/PW	0.816-0.888	0.864	0.030	0.009	2.3
PL/EL	0.381-0.427	0.409	0.019	0.006	3.2
PL/EW	1.050-1.170	1.110	0.056	0.017	3.4
PL/HW	0.833-0.938	0.894	0.040	0.012	2.9
PW/EL	0.446-0.500	0.474	0.019	0.006	2.7
PW/EW	1.240-1.350	1.290	0.057	0.017	3.0
PW/HW	0.989-1.090	1.030	0.049	0.015	3.2
EL/EW	2.570-2.830	2.720	0.105	0.031	2.6
EL/HW	2.100-2.310	2.190	0.086	0.026	2.6
EW/HW	0.750-0.856	0.804	0.039	0.012	3.3

limited to confirm this. I dc not have specimens from the Balkan Mountains but Obenbergers's description (in Louvet, 1925) suggests in the following summary that they might represent a mountain race: pronotum and elytra more coarsely punctate; elytra shorter, elytral pits slightly impressed, color very dark green or blue.

Derivation of specific epithet.- Latin uliginosus = of the marsh, referring to the habitat of members of this species.

Distribution.- Known from the British Isles, northern half of France to southern Scandinavia eastward to Yenisey River and Amur River, (I have seen specimens from Saroo in the Ural Mountains. These eastern records are reported from Bänninger (in Louvet 1925).) In the south this species is known from Italy in the central Apennine Mountains, the Balkan Mountains, Caucasus, Transcaucasus and Tien-shan Mountains (old Turkestan now part of Kirgiziya USSR and Sinkiang China). I have seen specimens from: France, Italy, Switzerland, Austria, Germany, Denmark, Sweden, Poland, USSR, as far east as the Tien-shan Mountains. I have seen 110 specimens, and dissected seven males.

Collecting notes.- On wet, sandy loam soil rich in mosses (Amblystegium, Paludela rarely Sphagnum). Other plants: small bullrushes (Juncaceae), sedges (Carexes) and Myrica gale (Lindroth, 1945).

Taxonomic notes.- I did not study the types, so I followed tradition in applying names. Schönherr did not

Table 4. Descriptive statistics for _E_. _uliginosus_ based on four males and seven females from central Italian Appennine Mountains.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.0	1.99	0.071	0.027	2.4
PW	2.1-2.4	2.27	0.135	0.054	4.0
EL	4.5-5.1	4.74	0.276	0.111	3.9
EW	1.7-1.8	1.76	0.092	0.037	3.5
Hw	2.2-2.4	2.29	0.102	0.041	3.0
B. Proportions.					
PL/PW	0.844-0.920	0.873	0.038	0.015	2.9
PL/EL	0.402-0.445	0.419	0.018	0.007	2.8
PL/EW	1.070-1.190	1.130	0.050	0.020	3.0
PL/HW	0.840-0.910	0.867	0.030	0.012	2.3
PW/EL	0.465-0.495	0.480	0.014	0.006	2.0
PW/EW	1.250-1.340	1.300	0.045	0.018	2.3
PW/HW	0.966-1.020	0.994	0.031	0.012	2.0
EL/EW	2.620-2.790	2.700	0.078	0.031	1.9
EL/HW	2.000-2.150	2.070	0.067	0.027	2.1
EW/HW	0.723-0.807	0.768	0.034	0.014	3.0

describe *E. latithorax* but Dejean saw the labelled specimen and used the name. Specimens of *E. bideli* and *E. viridicupreus* include the copper and brilliant green forms of the typical *E. uliginosus* in France. *E. impressifrons* is a name traditionally referred to this species. *E. italicus* refers probably to the Italian Appenine form, *E. uliginosus purkynei* refers to the Balkan population and *E. uliginosus laevisculptus* refers to the populations inhabiting the mountains of Tien-shan in the western Himalaya.

Geographical affinities.- I have seen specimens of this species as far east as northwestern China. If this is the eastern limit, then this species is sympatric only with *E. cupreus*, a member of the *cupreus* group. If reported correctly from Amur River, then it could be sympatric with *E. splendidus*, *E. sibiricus*, and *E. cupreus*.

Relationships.- Very closely related to the montane *E. pyrenaeus* as shown by the wide and twisted apex of the median lobe of male genitalia in dorsal view.

3.5.3.5 *Elaphrus pyrenaeus* Fairmaire and Laboulbène

Elaphrus pyrenaeus Fairmaire and Laboulbène 1854: 7. *Type locality*.- Haute-Pyrénés. Jeannel 1941: 218.

Elaphrus pyrenaeus nevadensis Jeanne 1966: 18. *Type locality*.- Puerto de la Ragua, Sierra Nevada, 1850 m Granada; type in Jeanne's collection, Bordeau, France; type seen by me.

Table 5. Descriptive statistics for E. pyrenaeus based on 10 males and 10 females from the French and Spanish Pyrenees.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.1	2.00	0.118	0.035	3.9
PW	2.1-2.4	2.27	0.150	0.045	4.4
EL	4.2-5.1	4.71	0.320	0.095	4.5
EW	1.5-1.9	1.73	0.171	0.051	6.6
HW	2.0-2.3	2.18	0.124	0.037	3.8
B. Proportions.					
PL/PW	0.856-0.930	0.879	0.032	0.010	2.4
PL/EL	0.404-0.456	0.425	0.020	0.006	3.2
PL/EW	1.060-1.330	1.150	0.084	0.025	4.9
PL/HW	0.878-0.964	0.916	0.031	0.009	2.3
PW/EL	0.450-0.511	0.484	0.023	0.007	3.2
PW/EW	1.220-1.430	1.310	0.078	0.023	3.9
PW/HW	1.000-1.080	1.040	0.035	0.011	2.3
EL/EW	2.530-3.000	2.710	0.158	0.047	3.9
EL/HW	2.070-2.240	2.160	0.079	0.023	2.4
EW/HW	0.723-0.828	0.796	0.040	0.012	3.3

Diagnostic combination.- This species is very closely related to E. uliginosus and adults of the two are distinguished as follows: upper surface brilliant green or brown copper metallic. Pronotum relatively longer: means of PL/PW and PL/HW significantly larger than E. uliginosus. Intervals 4, 6 and 8 smooth, not costate, and without or with suggested alveolae of microsculpture (Fig. 138).

Description.- Upper surface brilliant green metallic or in few specimens brilliant brown copper, ventral surface golden green metallic, and most of legs and palpi very dark blue. Pronotum relatively longer: means of PL/PW and PL/HW significantly higher than samples of E. uliginosus. Elytral pits deeply impressed (Fig. 120), lateral ridges narrowly outlined or absent, and intervals 4, 6 and 8 not costate.

Integument sculpture. Punctures similar in distribution to E. uliginosus but finer dorsally and denser ventrally, most adjacent punctures in contact on disc of proepisternum.

Meshes of microsculpture restricted dorsally. On elytra expressed at shoulder otherwise absent from intervals 4, 6 and 8 or indistinctly outlined (Fig. 138).

Male genitalia. Median lobe very similar to that of males of E. uliginosus, but apex in dorsal view more twisted (Fig. 44).

Measurements and proportions.- See Table 5.

Variation.- I found little noteworthy variation between the samples from the Pyrenees and the Sierra Nevada. However, the sample from the Sierra Nevada consists of two specimens. Thus until further material is obtained I prefer not to recognize *E. p. nevadensis*.

Derivation of specific epithet.- Latinization of the area of origin in the Pyrenee Mountains.

Distribution.- I have seen specimens from the French and Spanish Pyrenees and also the type from the Sierra Nevada. Jeanne (1966) reports them from the following Spanish provinces: Lerida, Huesca, Basses-Pyrénées, Navarra, Leon, Oviedo, and Segovia. Louvet (1925) reports them from the Alps and Beaujolais Mountains, but I have not seen these specimens. I have seen 32 specimens and dissected three males.

Collecting notes.- Found in subalpine and alpine mossy bogs (Jeanne, 1966).

Geographic affinities.- Presently, it is allopatric, but under colder climatic conditions, it is probably parapatric with *E. uliginosus* now only 300 km away.

Relationships.- Very closely related to *E. uliginosus* as shown by the wide and twisted apex of the median lobe of male genitalia in dorsal view.

3.5.3.6 *Elaphrus potanini* Semenov

Elaphrus potanini Semenov 1889: 352. *Type locality*.- China, province: Gan-ssu (Kansu in current spelling) at Amdo.

Adults. *Diagnostic combination*.- Dorsal surface bright brown copper; pits, pronotal postero-lateral angles, and anterior portion of head green metallic. Punctures dense and fine over dorsal surface. Main discal impression shallow. Otherwise quite similar to E. uliginosus adults.

Adults. Description.- Dorsal surface brown copper; elytral pits, postero-lateral angles of pronotum, and anterior portion of head green metallic; antennomeres 1 to 3, femur (except base), base of tibia and dorsal surface of tarsomeres golden-green metallic; base of femur and middle of tibia dark reddish brown; palpi brown. Pronotum very short, transverse and wider than head; lateral margin deeply sinuate; postero-lateral angles rather prominent and acute; anterior transverse stria very deeply impressed near middle; main discal impression slightly impressed; medial stria deep and short. Elytra elongate, pits well impressed, lateral ridges obsolete; mirrors not sharply outlined in intervals 3 and 5.

Derivation of specific epithet.- Named in honor of its collector, G. Potanin.

Distribution.- Known from a single specimen from the Chinese province of Kansu at Amdo. Collected on May 22, 1885.

Taxonomic notes.- This species is known to me only through Semenov's description. I included it in this group because of the deeply impressed anterior transverse stria of the pronotum, and also the transverse pronotum that is wider than the head. I believe it represents a distinct species because of its unusual coloration, its very short and transverse pronotum, and its longer elytra. Based on previous experience with Semenov's species, I trust his judgement.

Geographical affinities.- Probably allopatric in relation to all known members of Neoelaphrus.

Relationships.- I have not seen the type or any specimen. I am satisfied only to suggest its relationship to the uliginosus group. Examination of the type is necessary in solving this problem.

The fuliginosus group

Adults. Diagnostic combination.- Cornea of eye very thick (100 microns). Lateral margin of pronotum in lateral view not sinuate near middle, pronotal epipleuron not narrowest at middle (Fig. 18b); setae of posterior margin of fringe terminated 150 to 200 microns from postero-lateral angles (Fig. 182); bead of margin absent or wide (20 to 30 microns); anterior transverse stria clearly impressed but not ended submedially by longitudinal impression; surface with one large discal impression and one small submedial impression (two small barely outlined impressions antero-lateral to main discal impression in members of E. fuliginosus). Abdominal sterna 5 and 6 without or each with one or two accessory setae (Fig. 139). Tibia of foreleg of male with one small projection at base of apical spur and one large projection at base of posterior spur--best seen in posterior view (Fig. 149). Punctures on pleura and laterally on abdominal sterna large (30 to 45 microns), area near punctures widely depressed (diameter of depression about 80 microns)--best seen on proepisternum (Fig. 107). Apex of male median lobe in dorsal view very sharp (about 20 microns in width) and barely or not twisted.

Larvae. Diagnostic combination.- Common to all instars. Dorsal surface of parietale pale except near base of antennae and near frontal suture. Setae AII and AIE-I of mesonotum and metanotum large.

First instar larva. Meshes of microsculpture barely distinct baso-laterally on dorsal surface of parietale. Pointed sculpture absent or present on 2% of disc of mesonotum and metanotum near suture.

Characters common to second and third instar larvae. Epicranial suture short: 0.6 to 0.8 length of antennal scape. Pointed sculpture absent from dorso-lateral surface of parietale. Seta AM-P of tergum 10 very large.

Third instar larva. Size of prothoracic episternal and epimeral setae, and of metathoracic seta of anterior pleurite medium. Size of setae AII and AIM of terga 1 to 8 large, and of seta PII-P on terga 1 to 8 medium-small; no sculpture on urogomphus of tergum 9. Size of anterior seta of epipleuron of segments 1 to 7 large. Sternite of segment 1 with 12 accessory setae, of segments 2 to 7 each with 24, and of segment 8 with 34. Pointed sculpture on abdominal membrane in dorsal view extended narrowly around terga 1 to 8.

3.5.3.7 Elaphrus fuliginosus Say

Elaphrus fuliginosus Say 1834: 417. Type locality.- originally Pennsylvania, but Lindroth and Frietag (1969) designated a male neotype from Rumney, New Hampshire (MCZC). Say's name has been interpreted according to specimens in LeConte's collection (MCZC) by Lindroth (1961: 114 and 1969c: 332).

Adults. Diagnostic combination.- Adults are easily distinguished from those of E. cicatricosus and E. lindrothi by the very well developed lateral margin of the pronotum that is absent or barely suggested basally in members of the remaining two species and by the dark green metallic color of the dorsal surface that is very dark copper or dark brassy in members of the other two species. Specimens of E. fuliginosus are most likely to be confused with some members of the uliginosus group--especially with specimens of E. uliginosus. Adults of the two species are distinguished by characters mentioned under this group and by brown or reddish-brown tibiae and few setae (none to four) on abdominal segments 5 and 6.

Adults. Description.- Dorsal surface dark green except for purple pits, ventral surface very dark golden-green, but abdomen piceous; legs and palpi brown or reddish-brown with a green metallic hue. Body large, 9.5 to 10.3 mm (see Table 6 for measurements).

Pronotum with lateral margin completely beaded; head slightly wider than pronotum, narrower in few specimens; median longitudinal impression clearly impressed and extended briefly as anterior and posterior transverse striae; two barely suggested impressions antero-laterally to main discal impression. Intervals 3 and 5 of elytron each with sharply outlined rows of mirrors, these markedly contrasted against microsculpture, green and densely punctate intervals 4 and 6. Pits moderately impressed, lateral ridges narrow, and punctures abundant (20 to 25). Abdominal sternum 7 of males with numerous accessory setae, in females disc without or with one to three accessory setae.

Trochanter of foreleg with two setae. Femur of foreleg and midleg with about 60 setae, and of hind leg with about 10 setae. Tibia of midleg with large apico-internal projection between spurs; tibia of foreleg with about 25 setae (excluding setae of fringe), and of midleg and hind leg with about 80 setae.

Integument sculpture. Punctures of moderate size (20 to 30 microns) on coxae and scutellum, large (30 to 40 microns) on clypeus, head, pronotum and elytral intervals; and very large (40 to 45 microns) on thoracic pleura; and laterally

Table 6. Descriptive statistics for E. fuliginosus based on 10 males and 10 females from Brooklyn, New York.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	2.0-2.4	2.23	0.188	0.097	4.7
PW	2.2-2.6	2.45	0.143	0.043	3.9
EL	4.5-5.4	5.00	0.349	0.104	4.6
EW	1.5-2.0	1.84	0.139	0.041	5.0
HW	2.3-2.7	2.51	0.156	0.047	4.1
B. Proportions					
PL/PW	0.875-0.942	0.915	0.023	0.007	1.6
PL/EL	0.426-0.458	0.442	0.014	0.004	2.1
PL/EW	1.170-1.260	1.210	0.039	0.012	2.1
PL/HW	0.840-0.916	0.891	0.031	0.009	2.3
PW/EL	0.462-0.495	0.483	0.014	0.004	1.9
PW/EW	1.280-1.390	1.320	0.040	0.012	2.0
PW/HW	0.941-1.000	0.974	0.026	0.008	1.8
EL/EW	2.670-2.810	2.740	0.061	0.018	1.5
EL/HW	1.960-2.080	2.020	0.051	0.015	1.7
EW/HW	0.713-0.772	0.735	0.024	0.007	2.2

on thoracic and abdominal sterna. Punctures dorsally dense (20 to 80 microns apart), on elytral interval mostly 50 to 80 microns apart; and ventrally punctures on average 40 microns apart (10 to 80 microns apart); but laterally on abdominal sterna more scattered (40 to 120 microns apart). Punctures sharply outlined on 30 to 50% of circumference of dorsal surface, and on ventral surface slightly more distinctly impressed (50 to 70%) except medially on thoracic sternum.

Male genitalia. Apex of median lobe in lateral view narrow and ended ventro-apically by angular projection directed ventrally (Fig. 45).

Measurements and proportions.- See Table 6.

Variation.- I found no significant differences between far distant samples from Manitoba and Minnesota (20 specimens), and from Brooklyn, New York (20 specimens). Specimens of the western sample were slightly larger on average.

First Instar Larvae. Diagnostic combination.- Nasale toothed. Pointed sculpture on 5% of ventro-lateral surface of parietale; dorsal surface darker anteriorly, along frontale and occipital sutures. Pointed sculpture on surface of sternite 10.

First Instar Larvae. Description.- Nasale toothed. Dorsal surface of parietale pale except anteriorly near antennae, along frontale and occipital sutures;

microsculpture baso-laterally and restricted to small area near neck, pointed sculpture on 5% of dorsal surface near neck. Meshes of microsculpture on 15% of mesonotal and metanotal surface, and pointed sculpture on abdominal sternite 10. Pointed sculpture on 30% of lateral and ventral prothoracic surfaces, on abdomen less restricted as extended ventrally along hypopleura 2 to 8.

Second Instar Larvae. Diagnostic combination.- Sclerites less setose: pronotal epipleuron with one or two accessory setae, and urogomphus with about seven accessory setae. Microsculpture well developed on nota, terga and urogomphi.

Second Instar Larvae. Description.- Occipital suture shorter than antennal scape. Meshes of microsculpture dorsolaterally on parietale, but alveolae indistinctly outlined. Pronotal epipleuron with one or two accessory setae; disc of pronotum with meshes of microsculpture on 10% of surface. Mesonotal epipleuron with one accessory seta; meshes of microsculpture present on 40% of disc surface, pointed sculpture laterally on 10% of disc surface. Epipleuron of mesothorax with two accessory setae. Mesepimeron with one accessory seta. Metathorax as mesothorax. Terga 1 to 8 each with about 25 accessory setae, urogomphus of tergum 9 with about seven accessory setae (Fig. 98b), tergum 10 without major and with one minor accessory seta; pointed sculpture more restricted on tergum 1; on urogomphus clearly outlined and shaped as small scales, sculpture on tergum 10 multipointed. Pointed sculpture present on 5% of posterior band surface of terga 1 to 8 and on 10% of anterior band of tergum 9. Epipleuron and hypopleuron of terga 2 to 8 each with about eight accessory setae. Sternite of segment 8 with about 15 accessory setae; pointed sculpture extended on entire surface of segment 10. External poststernite of segment 1 with two and of segments 2 to 7 each with four accessory setae. Pointed sculpture of membrane clearly outlined and expanded ventrally on abdomen.

Third Instar Larvae. Diagnostic combination.- Sclerites generally less setose: posterior band of mesonotum and metanotum without lateral accessory setae, urogomphus with about seven setae. Sculpture clearly developed over terga and nota.

Third Instar Larvae. Description.- Disc of pronotum with about 20 accessory setae; major accessory setae on row behind posterior row of basic setae medium-small, major accessory setae on pronotal epipleuron medium-small; meshes of microsculpture absent from disc. Disc of mesonotum with about 85, and mesonotal epipleuron with nine accessory setae; meshes of microsculpture present on 25% of disc surface. Mesepipleuron with two accessory setae. Mesosternite without accessory setae. Metathorax as mesothorax. Main knobs on urogomphus of tergum 9 large in lateral view (Fig. 98c); terga 1 to 8 each with about 70 and urogomphus of tergum 9 with about seven accessory setae; pointed sculpture on 5% of anterior band of terga 1 to 8, and on 20% of anterior band of tergum 9, sculpture absent or barely suggested on urogomphus. Epipleuron of segments 2 to 8 each with 30 accessory setae, pointed sculpture of segments 2 to 9 very fine. Hypopleuron of segments 1 to 8 each with 25 accessory setae. Sternite of segment 10 with 12 minor accessory setae. External poststernite of segment 1 with eight and of segments 2 to 7 each with 14 accessory setae. Internal poststernite of segment 1 with two and of segments 2 to 7 each with four accessory setae.

Derivation of specific epithet.- From latin meaning blacken or darken.

Distribution.- From the Atlantic coast of Maine to Maryland west to Manitoba, and Nebraska (Fig. 158). I examined 275 adults, three first instar, one second instar and one third instar larvae from Vermont. I dissected five males.

Collecting notes.- According to Larochelle (1975) found in open places with no or scattered vegetation on wet sandy soil. I found two specimens on a similar habitat.

Geographical affinities.- This species is sympatric with all members of the uliginosus group at least in Maryland. Thus, it overlaps completely E. cicatricosus and overlaps only the eastern range of E. lindrothi. It is also sympatric with E. clairvillei and E. olivaceus in the northern half of its range.

Relationships.- This is the most conservative member of the group. It is related to the sister group formed by the remaining members -- E. lindrothi and E. cicatricosus. These last species share the lack of bead on the lateral margin of the pronotum.

3.5.3.8 Elaphrus cicatricosus LeConte

Elaphrus cicatricosus LeConte 1848: 448. Type locality.- Central New York State; type in Museum of Comparative Zoology, Harvard, Massachussetts; seen by Lindroth (1961). Lindroth 1961: 114.

Elaphrus rhodeanus Casey 1924: 17. Type locality.- Boston Neck, Rhode Island; type in United States National Museum, Washington D.C.; type seen by Lindroth (1961) and myself. Lindroth 1961: 114.

Adults. Diagnostic combination.- Adults are easily recognized by the scattered punctures dorsally, the very dark copper dorsal color, the very rugose appearance of the pronotum, absent or barely suggested lateral margin of pronotum, and the very large lateral ridges in pits of elytra. Specimens are easily separated from members of E. lindrothi by the larger and less densely punctate surface of its members, otherwise adults of E. cicatricosus are similar to members of E. cupreus and E. japonicus but are easily separated from others by the form of the pronotum outline.

Adults. Description.- Dorsal surface very dark copper except for purple pits, ventral surface black and abdominal sterna dark piceous, legs brown with green metallic hue on femur and blue metallic hue on tibia and tarsomeres. Body large, length 8.8 to 9.2 mm (see Table 7 for measurements).

Pronotum with lateral margin in vertical plane rounded or barely angulate; head slightly wider than pronotum width; pronotal medial stria short and anterior transverse stria indistinctly outlined; disc without antero-lateral impression. Intervals 3 and 5 with rows of sharply outlined mirrors, but mirrors little contrasted against very dark and sparsely punctate intervals 4 and 6. Pits clearly impressed and extremely well outlined by large lateral convex ridges, each pit with four to eight punctures. Abdominal sternum 7 of males and females without or with one or two accessory discal setae.

Trochanter of foreleg with one seta. Femur of foreleg and midleg with about 30 setae, and of hind leg with six setae. Tibia of midleg of males with large apico-internal projection between spurs; tibia of foreleg with about 20 setae and of midleg and hind leg with about 55 setae.

Integument sculpture. Punctures moderate in size (20 to 30 microns) on coxae and large (30 to 40 microns) to very large (40 to 45 microns) dorsally and ventrally, irregularly scattered over dorsal surface (10 to 200 microns apart) except slightly denser ventrally on pleura (10 to 90 microns apart), and on thoracic and abdominal sterna 70 to 150 microns apart; sharply outlined on 30% of circumference on clypeus, head, and pronotum, coxae and elytral epipleuron, but indistinctly outlined on elytral intervals 4, 6 and 8, and sharply outlined on 50% of pleura and thoracic and abdominal sterna.

Alveolae of microsculpture subconvex on dorsal surface except convex in pits, and postero-lateral impression of pronotum, absent or suggested on mirrors; alveolae flat ventrally.

Male genitalia. Apex in lateral view very large and slightly enlarged ventrally (Fig. 47).

Measurements and proportions.- See Table 7.

Variation.- I found no significant differences between means of samples from northern New York (20 specimens) and New Jersey (20 specimens).

First Instar Larvae. _Diagnostic combination_.- Teeth of nasale absent. Pointed sculpture absent ventro-laterally from parietale; parietale dark area more restricted: absent from occipital suture. Pointed sculpture absent from sternite 10.

First Instar Larvae. _Description_.- Nasale not toothed. Dorsal surface of parietale pale except anteriorly near antennae and internal to system DMM; meshes of microsculpture dorso-laterally near neck present, pointed sculpture absent. Meshes of microsculpture present on 10 to

Table 7. Descriptive statistics for *E. cicatricosus* based on 10 males and 10 females from Maclean Bog, New York.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	2.0-2.3	2.11	0.116	0.035	3.7
PW	2.2-2.5	2.32	0.135	0.040	3.9
EL	4.5-5.2	4.86	0.270	0.080	3.7
EW	1.6-1.9	1.97	0.129	0.038	4.8
HW	2.3-2.6	2.44	0.106	0.032	2.9
B. Proportions.					
PL/PW	0.872-0.966	0.909	0.033	0.010	2.4
PL/EL	0.422-0.454	0.435	0.019	0.005	2.4
PL/EW	1.130-1.240	1.190	0.050	0.015	2.8
PL/HW	0.828-0.911	0.865	0.026	0.008	2.0
PW/EL	0.454-0.510	0.479	0.020	0.006	2.7
PW/EW	1.250-1.370	1.310	0.061	0.018	3.1
PW/HW	0.907-0.990	0.952	0.030	0.009	2.1
EL/EW	2.620-2.840	2.740	0.099	0.029	2.4
EL/HW	1.900-2.060	1.990	0.065	0.019	2.2
EW/HW	0.697-0.767	0.726	0.032	0.009	2.9

12% of disc of mesonotum and metanotum; pointed sculpture absent from disc of sternite 10. Pointed sculpture of membrane more restricted: extended over 15% of lateral surface of thorax and not extended ventrally along hypopleuron.

Second Instar Larvae. Diagnostic combination.- Sclerites very setose: pronotal epipleuron with seven accessory setae, and urogomphus with about 25 accessory setae. Sculpture absent from nota, very restricted on terga, and suggested on urogomphi of tergum 9.

Second Instar Larvae. Description.- Occipital suture 0.67 length of antennal scape. Meshes of microsculpture indistinct laterally on dorsal surface of parietale. Pronotal epipleuron with seven accessory setae; disc of pronotum without sculpture. Mesonotal epipleuron with five accessory setae; disc without sculpture. Metathorax as mesothorax. Terga 1 to 8 each with 36 accessory setae, urogomphus of tergum 9 with 25 (Fig. 99a), and tergum 10 with two major and four minor accessory setae; pointed sculpture on only 5% of disc, urogomphus pointed sculpture indistinct, sculpture of tergum 10 single-pointed, pointed sculpture absent from posterior band of terga 1 to 8 and from anterior band of tergum 9. Epipleuron and hypopleuron of segments 1 to 8 each with about 25 accessory setae. Sternite 8 with 22 accessory setae, sternite 10 with 10 minor accessory setae; pointed sculpture absent from segment

10. External poststernite of segment 1 with four and of segments 2 to 7 each with seven accessory setae. Pointed sculpture on membrane fine and more restricted dorsally to surfaces near lateral and basal margin of terga 1 to 8.

Third Instar Larvae. Diagnostic combination.- Sclerites setose: posterior band of mesonotum and metanotum with five to 15 accessory setae laterally, urogomphus of tergum 9 with about 30 accessory setae. Sculpture absent from nota and membrane, and very restricted on terga.

Third Instar Larvae. Description.- Disc of pronotum with about 40 accessory setae; major accessory setae on row behind posterior row of basic setae medium, and major accessory setae on pronotal epipleuron medium; meshes of microsculpture absent from disc. Disc of mesonotum with more than 100 accessory setae. Mesosternite with three accessory setae. Metathorax as mesothorax. Main knobs of urogomphus of tergum 9 medium in lateral view (Fig. 99b); terga 1 to 8 each with about 140 and urogomphus with about 30 accessory setae; pointed sculpture absent from urogomphus and anterior band of terga 1 to 9. Epipleuron of segments 2 to 8 each with 40 to 60 accessory setae; pointed sculpture absent from segments 1 to 9. Hypopleuron of segments 1 to 8 each with 25 to 50 accessory setae. Sternite 10 with six minor accessory setae. External poststernite of segment 1 with 15 and of segments 2 to 7 each with 18 accessory setae. Internal poststernite of segment 1 with five and of segments 2 to 7 each with seven accessory setae.

Derivation of specific epithet.- From Latin meaning "scarred" probably referring to very rugose dorsal surface.

Distribution.- The range extends in the north from Michigan, Quebec and Maine, southwest to Tennessee and Maryland (Fig. 159). I examined 250 adults and dissected four males. I studied three first instar, three second instar, and three third instar larvae from Maclean Bog, New York.

Collecting notes.- I found these beetles in various localities on very wet, relatively firm organic mud near slow-flowing brooks where alders grow commonly, usually in the shade of larger trees. These observations fit very well with Lindroth's and Darlington's experience (Lindroth, 1961: 114).

Geographical affinities.- The ranges of *E. fuliginosus* and this species overlap nearly completely. At the southeast end of its range this species is sympatric with *E. lindrothi*. In the northern half of its range, *E. cicatricosus* overlaps with *E. clairvillei* and *E. olivaceus*, both members of the *cupreus* group.

Relationships.- Closely related to *E. lindrothi* as shown by the lack of bead on the lateral margin of the pronotum, and of accessory setae on abdominal sternum 7 of males.

3.5.3.9 Elaphrus lindrothi new species

Elaphrus lindrothi new species. Type material.- Holotype male and allotype female labelled; "Bowie Md, May 5, 62, Mud flat: (USNM)." Six additional paratypes from three localities, listed below.

Elaphrus cicatricosus Blatchley 1910: 49, not LeConte.

Adults. Diagnostic combination.- Adults of this species are easily recognized by the very dark silvery-brass dorsal color, the denser and finer (20 to 25 microns) dorsal punctation (Fig. 104 and 121), pronotal lateral margin in vertical plane rounded or barely angulate, the single row of sutural mirrors of interval 3, and the barely suggested or absent lateral ridges of the elytral pits. Members of this species resemble not so much E. cicatricosus but members of the subgenus Elaphrus, especially dark specimens of E. ruscarius.

Adults. Description.- Dorsal surface very dark silvery-brass, ventral surface black or dark brown, abdominal sterna brown, legs, palpi and antennomeres 1 to 3 reddish brown, femurs, tibia, and tarsomeres with slightly purple metallic hue.

Pronotal lateral margin in vertical plane rounded or barely angulate; head wider than pronotum; medial longitudinal impression shallow but with clearly outlined anterior and posterior transverse impressions, disc with one large and one small impression. Only mirrors of interval 3 outlined, mirrors contrasted but not too sharply outlined. Pits of elytra impressed, lateral ridges absent or barely suggested (Fig. 104), pits with about 10 to 15 punctures. Abdominal sternum 7 of males and females without accessory setae on disc. Trochanter of foreleg with two setae. Femur of foreleg and midleg with about 30, and of hind leg with about five accessory setae. Tibia of midleg of males with large projection apico-internally between spurs; tibia of foreleg with about 20, and of midleg and hind leg with about 55 setae.

Integument sculpture. Punctures of moderate size (20 to 25 microns) on coxae, clypeus, head, pronotum and elytral intervals; large (30 to 35 microns) on thoracic pleura and laterally on thoracic and abdominal sterna, quite uniformly distributed dorsally -- 10 to 30 microns apart on head and elytral intervals 4, 6 and 8 (Fig. 121); and 20 to 40 microns apart on pronotum (Fig. 104); ventrally, 20 to 90 microns apart; sharply outlined on 30% of circumference of clypeus, head, pronotum and elytral intervals, and on 50% of pleura, and laterally on thoracic and abdominal sterna.

Alveolae of microsculpture subconvex dorsally and on pleura of prothorax and mesothorax. On remaining ventral surface alveolae flat.

Male genitalia. Apex of median lobe in lateral view very similar to those of _E_. _fuliginosus_: apex narrow and terminated ventrally with angular ventral projection

Table 8. Descriptive statistics for *E. lindrothi* new species based on three males and five females from southern Indiana and Maryland.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-2.0	1.83	0.132	0.062	4.8
PW	1.7-2.1	1.87	0.195	0.092	6.6
EL	3.8-4.4	4.15	0.346	0.163	5.6
EW	1.5-1.7	1.61	0.148	0.070	6.1
HW	2.0-2.3	2.18	0.136	0.064	4.2
B. Proportions.					
PL/PW	0.878-0.973	0.929	0.052	0.025	3.7
PL/EL	0.415-0.477	0.440	0.029	0.014	4.4
PL/EW	1.060-1.220	1.130	0.079	0.037	4.7
PL/HW	0.820-0.851	0.839	0.016	0.008	1.3
PW/EL	0.441-0.503	0.475	0.030	0.014	4.2
PW/EW	1.170-1.290	1.220	0.072	0.034	3.9
PW/HW	0.852-0.953	0.905	0.051	0.024	3.8
EL/EW	2.490-2.680	2.570	0.093	0.044	2.4
EL/HW	1.780-1.980	1.910	0.100	0.047	3.5
EW/HW	0.698-0.779	0.742	0.042	0.020	3.8

directed anteriorly (Fig. 46).

Measurements and proportions.- See Table 8.

Variation.- Samples from southern Indiana and Maryland were too small for analysis. These samples appear to be similar.

Derivation of specific epithet.- I name this species in honor of Prof. C. H. Lindroth, who not only contributed immensely to a better understanding of North American carabids but also laid a solid foundation for further study of the Elaphrini.

Distribution.- Known from northeastern United States (Fig. 159). Localities are listed below.

United States.- MARYLAND: Priest Bridge (1;USNM), Bowie (2; USNM) INDIANA: Knox County (4; PURC), Hovey Lake (1;PURC).

Collecting notes.- Blatchley (1910) in his work on beetles of Indiana had only specimens of this species, having collected them on mud flats at border of Bald Cypress swamp. The habitat at Hovey Lake was the same where a specimen was collected on wet clay with no vegetation, in the shade of Bald Cypress trees. I have one teneral specimen collected on September 2. Thus adults probably overwinter.

Geographical affinities.- The western part of the range of this species is south of the range of the two other species of the fuliginosus group, but in the eastern side of the range, it overlaps the southern end of the ranges of E. fuliginosus and E. cicatricosus.

Relationships.- Closely related to *E*. *cicatricosus* as shown by the lack of bead along the lateral margin of the pronotum, and the lack of accessory setae on abdominal sternum 7 of males.

The *cupreus* group

Adults. *Diagnostic combination*.- Cornea of eye thickness normal (45 to 60 microns). Pronotum with lateral margin beaded; bead very narrow (10 to 15 microns in width); disc with one or two discal impressions; submedial one present or absent; setae of fringe along posterior margin terminated far (200 microns or more) from postero-lateral angles (Fig. 19). Prosternum punctures smaller (25 to 30 microns in size) and surrounding surface narrowly impressed or not. Abdominal sterna 5, 6 and 7 with many accessory setae in most members or without or with one to two accessory setae. Tibia of foreleg in males without sharp and large projection at base of posterior spur.

Larvae. *Diagnostic combination*.- Common to all instars. Dorsal surface of parietale mostly dark on disc. Setae AII and AIE-AI of mesonotum and metanotum medium-large.

First instar larva. Meshes of microsculpture distinct baso-laterally on dorsal surface of parietale. Pointed sculpture on 10% of disc of mesonotum and metanotum near suture.

Characters common to second and third instar larvae. Epicranial suture as long as antennal scape. Pointed sculpture on 15% of dorso-lateral surface of parietale. Seta AM-P of tergum 10 large or smaller.

Third instar larva. Seta of proepisternum and proepimeron, and of anterior pleurite of metathorax medium-small. Setae AII and AIM of terga 1 to 8 medium, and seta PII-P of terga 1 to 8 small to very small; pointed sculpture present on urogomphus of tergum 9. Anterior seta of epipleuron of segments 2 to 7 medium. Abdominal sternite 1 with four, and sternites 2 to 8 each with 18 accessory setae. Pointed sculpture on abdominal membrane in dorsal view expanded widely around terga 1 to 8.

3.5.3.10 *Elaphrus sibiricus* Motschulsky

Elaphrus sibiricus Motschulsky 1844: 71. *Type locality*.- probably Irtysh River. Nakane 1973: 4.

Elaphrus dauricus Morawitz 1863: 191. *Type locality*.- probably Dauria. Bänninger 1917: 147.

Adults. *Diagnostic combination*.- In details of the dorsal surface, adults of this species resemble the greener adults of *E*. *clairvillei* and of *E*. *olivaceus*, but the former is easily distinguished from these and remaining species by a combination of dense dorsal punctures (30 to 35 microns apart on side of pronotum and 25 to 35 microns apart on elytral intervals 4, 6 and 8) and larger punctures (20 to 30 microns in size). Males are easily recognized by unusual apex of median lobe which, in dorsal view, is very elongate in front of the internal sac, and, in lateral view, very wide and angular at apex (Fig. 48).

Adults. Description.- Upper surface brilliant green in impressions, dark green or bronze-green elsewhere except for purple pits; ventral surface very dark golden-green metallic to nearly black medially; legs and palpi piceous except for green metallic reflection on femur, on apex of tibia dorsally and on dorsal surface of tarsomeres. Mentum tooth moderately emarginate; emargination 0.5 length of tooth. Disc of pronotum with two impressions. Prosternal process with one to six accessory setae. Metasternum medially with few punctures, all setose. Abdominal sterna 5 and 6 each with five to 10 accessory setae, sternum 7 in males with about 10 to 20 accessory setae and in females with 10 or less accessory setae. Setigerous punctures of elytra very distinctly outlined; elytral pits well impressed with eight to 12 punctures; lateral ridges of pits not fused anteriorly and posteriorly, ridges wide. Mirrors outlined on intervals 3 and/or 5. Number of setae on legs not studied in detail but similar to members of E. clairvillei. Tibia of midleg of males with sharp apico-internal projection between spurs (Fig. 150). External 0.5 of hind coxa with punctures, internal 0.33 with eight to 15 accessory setae.

Integument sculpture. Punctures moderate (20 to 25 microns in size) on clypeus, head, pronotum and elytral intervals 4, 6 and 8, large (30 to 35 microns in size) on pleura and laterally on thoracic and abdominal sterna. Punctures densely distributed (25 to 40 microns apart) on clypeus, head pronotum (side) and elytral intervals 4, 6 and 8, moderately dense (30 to 50 microns apart) on pleura and laterally on thoracic and abdominal sterna; generally sharply outlined on 30 to 50% of circumference.

Alveolae of microsculpture on head, pronotum and elytral intervals 4, 6 and 8 subconvex, and ventrally on pleura and thoracic and abdominal sterna subconvex or convex.

Male genitalia. Apex of median lobe in lateral view very wide and ended ventrally as angular projection (Fig. 48b); in dorsal view apex not twisted, relatively wide (40 microns) and extended far posteriorly to apex of internal sac (Fig. 48a).

Measurements and proportions.- See Table 9.

Variation.- I could not study this aspect as I had too few specimens.

Derivation of specific epithet.- From latin for Sibiria, the area of origin of the type.

Distribution.- Specimens of this species are known from eastern Sibiria, Mongolia, northeastern China and northern Japan. I have seen them from the following localities: USSR: Baikal Lake (UASM, MCZ, BMNH), Tschita (MCZ), Amur River (BMNH), and Ussuri River (MCZ); CHINA; Hailar (MCZ): JAPAN:

Table 9. Descriptive statistics for E. sibiricus based on nine males and five females from eastern Sibiria, northeastern China and Northern Japan.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-2.1	1.98	0.150	0.053	5.0
PW	2.1-2.4	2.28	0.157	0.055	4.6
EL	4.5-5.2	4.89	0.256	0.091	3.5
EW	1.6-1.8	1.74	0.105	0.035	4.0
HW	2.1-2.4	2.27	0.120	0.043	3.5
B. Proportions.					
PL/PW	0.805-0.910	0.869	0.045	0.016	3.5
PL/EL	0.385-0.421	0.404	0.015	0.005	2.5
PL/EW	1.060-1.180	1.130	0.054	0.019	3.2
PL/HW	0.841-0.899	0.871	0.029	0.010	2.2
PW/EL	0.437-0.480	0.466	0.017	0.006	2.5
PW/EW	1.260-1.330	1.300	0.034	0.012	1.7
PW/HW	0.943-1.050	1.000	0.047	0.017	3.1
EL/EW	2.740-2.880	2.800	0.072	0.028	1.7
EL/HW	2.090-2.220	2.150	0.056	0.020	1.7
EW/HW	0.742-0.811	0.769	0.031	0.011	2.7

Rebun Island. I have examined nine males and five females.

Collecting notes.- One specimen was found on a stream bank (Ball pers. comm.). I have one male collected in mid-August with slightly tanned median lobe, thus overwintering is probably in adult stage.

Geographical affinities.- Found sympatrically in northern China with *E. cupreus*. It is also sympatric with *E. splendidus* and *E. japonicus*, both members of the *uliginosus* group.

Relationships.- Closely related to *E. cupreus* as shown by the very long and wide apex of the median lobe of the males.

3.5.3.11. *Elaphrus cupreus* Duftschmid

Elaphrus cupreus Duftschmid 1812: 194. *Type locality*.- probably Germany. Dejean 1826: 271.

Elaphrus arcticus Dejean 1826: 272. *Type locality*.- Lapland.

Adults. *Diagnostic combination*.- Adults are easily recognized among members of this group by the dark bronzy-copper dorsal surface, the less densely punctate intervals 4, 6 and 8, and subconvex alveolae of microsculpture on head, pronotum and intervals 4, 6 and 8 (Fig. 132).

Adults. *Description*.- Upper surface dark bronzy-copper except for purple pits; ventral surface very dark golden green; legs and palpi piceus except for dark green hue on femur; upper surface of tibia (apex) and tarsomeres purple.

Mentum tooth moderately emarginate: emargination 0.5 length of tooth. Pronotum with two discal impressions. Prosternal process in most members with one to four accessory setae. Most punctures antero-medially on metasternum with setae. Punctures few laterally on abdominal sternum 7. Abdominal sterna 5 and 6 each with five to 15 accessory setae, and sternum 7 in males with about 20 accessory setae in females with five to 10 accessory setae. Setigerous punctures of elytra very distinctly outlined. Pits of elytra deeply impressed, lateral ridges wide and not fused anteriorly and posteriorly. Punctures in sutural pits numerous (15 to 25). Mirrors outlined on intervals 3 or 3 and 5. Number of setae on legs not studied in detail, similar to members of _E_. _clairvillei_. Tibia of midleg of males with sharp apico-internal projection between spurs. Hind coxae with few punctures on external 0.5, and with three to five accessory setae near internal margin.

Integument sculpture. Punctures moderate (20-25 microns) on clypeus, head, pronotum and elytral intervals 4, 6 and 8, large (30 microns) on pleura and laterally on thoracic and abdominal sterna. Punctures scattered (50 to 150 microns apart) on head, pronotum (side) and elytral intervals 4, 6 and 8; moderately dense (30 to 50 microns apart) on pleura and laterally on thoracic and abdominal sterna. Punctures sharply outlined on 30 to 50% of circumference.

Alveolae of microsculpture on head, pronotum and elytral intervals 4, 6 and 8 subconvex, and ventrally on pleura and thoracic and abdominal sterna subconvex or convex.

Male genitalia. Apex of median lobe in lateral view very wide and terminated at apex subangularly (Fig. 49b); in dorsal view apex not twisted, relatively wide (40 microns) and extended far posteriorly from apex of internal sac (Fig 49a).

Measurements and proportions.- See Tables 10 and 11.

Variation.- Specimens from southern Sweden resemble closely those from Germany and western Russia (Kaluga near Moscow) and France. Four specimens from arctic Scandinavia seem smaller. My single specimen east of the Caspian Sea seems typical, though darker. Three specimens from northeastern China seem different and smaller. Analysis of ratios suggests the same pattern: samples of specimens from southern Sweden, Germany and western Russia are similar or show inconsistent significant differences in one or two means. Differences between samples from southern Sweden and France are more marked, as three means are significantly different: PL/HW, EL/EW, and EL/HW. These differences are inconsequential taxonomically since the Moscow and German samples differ little or not at all from the French sample. I suspect the variation observed might reflect local adaptation. The results suggest that gene flow exists among these populations. The arctic Scandinavian sample is

Table 10. Descriptive statistics for *E. cupreus* based on 10 males and 10 females from southern Sweden--SKANE: Lomma Silvakra(USNM).

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-2.0	1.93	0.119	0.035	4.1
PW	1.9-2.4	2.10	0.140	0.042	4.4
EL	4.5-5.0	4.81	0.213	0.063	3.0
EW	1.6-1.8	1.76	0.111	0.033	4.2
HW	2.1-2.3	2.22	0.097	0.029	2.9
B. Proportions.					
PL/PW	0.843-1.010	0.922	0.054	0.016	3.9
PL/EL	0.383-0.430	0.402	0.018	0.005	3.0
PL/EW	1.030-1.250	1.100	0.077	0.023	4.7
PL/HW	0.814-0.910	0.869	0.040	0.012	3.0
PW/EL	0.408-0.461	0.436	0.020	0.006	3.1
PW/EW	1.130-1.330	1.190	0.065	0.019	3.6
PW/HW	0.893-0.978	0.943	0.039	0.012	2.8
EL/EW	2.650-2.910	2.730	0.094	0.028	2.3
EL/HW	2.070-2.270	2.160	0.065	0.019	2.0
EW/HW	0.711-0.831	0.793	0.040	0.012	3.3

composed of smaller specimens, but the sample is too small to draw conclusions. The sample from northeastern China not only is made of smaller specimens but the ratio PL/EL is unusually high (average of three specimens 4.1), as elytra are relatively shorter; unfortunately this sample is too small for conclusions. My general impression is that gene flow exists between all European populations, and the only suggested structural shift is from the northeastern Chinese sample.

Derivation of specific epithet.- From Latin "cupreus" meaning copper referring to the dorsal color that is very dark copper.

First Instar Larvae. Diagnostic combination.- The larvae of this species are very similar to those of *E. clairvillei* and are distinguished by the most restricted meshes of microsculpture on dorsal surface of parietale (7% of surface) and ventrally meshes very close to neck.

First Instar Larvae. Description.- Seta MP of frontale small. Seta DMM-A and DMP-A of parietale medium; meshes of microsculpture narrowly extended on dorsal surface from neck toward occipital suture, and ventrally restricted to neck area; pointed sculpture extended over 5% of dorsal and ventral surface. Seta AII-E on pronotum medium; dorsal surface of disc without sculpture. Meshes of microsculpture on 20% of disc of mesonotum; pointed sculpture near suture on 7% of disc of mesonotum and on 15% of disc of metanotum,

Table 11. Descriptive statistics for E. cupreus based on 10 males and 10 females from Marne Region, France.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.0	1.91	0.100	0.030	3.4
PW	2.0-2.2	2.12	0.108	0.032	3.4
EL	4.6-5.1	4.78	0.192	0.059	2.7
EW	1.7-1.9	1.79	0.108	0.032	4.0
HW	2.2-2.4	2.26	0.077	0.023	2.3
B. Proportions.					
PL/PW	0.849-0.964	0.904	0.041	0.012	3.0
PL/EL	0.376-0.430	0.400	0.022	0.006	3.6
PL/EW	0.948-1.160	1.070	0.078	0.023	4.9
PL/HW	0.793-0.899	0.840	0.035	0.010	2.8
PW/EL	0.422-0.478	0.443	0.023	0.007	3.4
PW/EW	1.120-1.280	1.180	0.071	0.021	4.0
PW/HW	0.880-0.978	0.930	0.033	0.010	2.3
EL/EW	2.520-2.750	2.670	0.082	0.024	2.0
EL/HW	1.980-2.170	2.100	0.074	0.022	2.3
EW/HW	0.734-0.837	0.786	0.041	0.012	3.5

on 5% of lateral area of discs of both nota, and absent from posterior band of both nota. Setae AII and AIM of terga 1 to 8 medium-small; pointed sculpture of urogomphus of tergum 9 indistinctly outlined. Pointed sculpture on abdominal sternite 10. Pointed sculpture of thoracic membrane on ventral surface restricted to 20%, on prothorax not extended toward episternum, and on abdomen present around hypopleuron of segments 2 to 7.

Second Instar Larvae. Diagnostic combination.- Similar to larvae of E. clairvillei but distinguished as follows: meshes of microsculpture indistinctly outlined on 50% of disc of pronotum; pointed sculpture on ventral surface of abdominal membrane not extended toward sternites 2 to 7, but extended behind poststernites. These larvae differ from those of E. olivaceous and E. laevigatus by the pointed sculpture near suture on 2% of mesonotum and on 10% of metanotum and laterally on 15% of disc of both nota.

Second Instar Larvae. Description.- Meshes of microsculpture on dorsal surface of parietale basolaterally; pointed sculpture on 15% of dorsal surface near neck; ventrally meshes on 5% of surface and pointed sculpture absent. Major accessory setae of pronotal epipleuron medium-small; meshes of microsculpture on 40% of mesonotum surface. Pointed sculpture near suture on 2% of disc of mesonotum and on 10% of disc of metanotum, laterally on 15% of disc of both nota, and absent from mesepisternum and metepisternum. Tergum 2 and following covered with microsculpture. Pointed sculpture on urogomphus of tergum 9 distinctly outlined and nearly scale-like, and pointed sculpture present on 10% of anterior band. Pointed sculpture on tergum 10 distinctly outlined. Pointed sculpture on abdominal membrane extended toward sternites 2 to 7 and behind poststernite.

Third Instar Larvae. _Diagnostic combination_.- Similar to larvae of _E_. _clairvillei_ but distinct as follows: pointed sculpture absent near suture of mesonotum and on 3% only on metanotum; pointed sculpture very restricted on terga 1 to 5. These larvae are distinct from remaining members as follows: pointed sculpture extended over 60% of anterior band of tergum 9; abdominal sternite 9 with more accessory setae (six); and pointed sculpture present on 5% of posterior band of terga 1 to 8.

Third Instar Larvae. _Description_.- Meshes of microsculpture absent from disc of pronotum. Pointed sculpture absent near suture from disc of mesonotum but present on 3% of disc of metanotum, and present laterally on 10% of both nota; on 5% of anterior and posterior bands of terga 1 to 8 and on 60% of anterior band of tergum 9. Tergum 6 and following entirely covered with microsculpture. Abdominal sternite 9 with six accessory setae. Pointed sculpture of membrane markedly expanded.

Distribution.- The range of this species extends over most of boreal and cold temperate Eurasia: from arctic Scandinavia to central France, northern Italy, Yugoslavia, and eastward across Siberia to northeastern China (Lindroth, 1945). I have seen specimens from Europe (Norway, Sweden, Finland, Denmark, Russia, Poland, Germany, England, Ireland, Holland, Belgium, France, Switzerland, Austria, Czechoslovakia, and Hungary), east of the Caspian Sea (Geok-tapa) and from northeastern China (Manchuria). I examined 500 adults, three first instar, four second instar and two third instar larvae from Austria.

Collecting notes.- Adults live on wet organic mud on surfaces without vegetation or scattered vegetation in mainly shady situations, near small rivers, large lakes, small pools and also in marshy areas of forests. They are absent from pure inorganic soil but occur on moss though rarely on *Sphagnum* moss. Populations are known from the alpine zone of Norway and Finland but not from tundra. (Lindroth, 1945: 461).

Geographical relationships.- This species is sympatric with *E. sibiricus*, a member of the *cupreus* group and with *E. uliginosus* and probably with *E. splendidus*, both in the *uliginosus* group.

Relationships.- Related to *E. sibiricus* as shown by the shared elongate and wide apex of the median lobe of males.

3.5.3.12 Elaphrus clairvillei Kirby

Elaphrus clairvillei Kirby 1837: 61. Type locality.- Lake Nipigon, Ontario, restricted by Lindroth 1961: 112; type (seen by Lindroth) in British Museum of Natural History, London, England. Lindroth 1961: 112.

Elaphrus politus LeConte 1850: 209. Type locality.- Maple Island, Ontario (northwest of Sault Ste. Marie); type (seen by Lindroth and me) in Museum of Comparative Zoology, Cambridge, Massachussets; Lindroth 1961: 112.

Elaphrus frosti Hippisley 1922: 64. Type locality.- Terrace, British Columbia; type supposed to be in Frost's collection, but not seen by Lindroth or me. Lindroth 1961: 112.

Elaphrus torreyensis Tanner 1941: 137. Type locality.- Torrey, Wayne Co., Utah; type (seen by Lindroth) in Brigham Young University, Provo, Utah; Lindroth 1961: 112.

Elaphrus clairvillei lynni Pierce 1948b: 52. Type locality.- Lynne Creek, British Columbia; type (seen by me) in the Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

Adults. Diagnostic combination.- Adults of this species are easily distinguished from those of E. sibiricus and E. cupreus by fused lateral ridges of elytral pits (Fig. 133), thus the ridges are ring-shaped; by presence of one discal impression on pronotum (two impressions very rare) and by barely expressed or barely suggested meshes in spots or absence of meshes from most of head, pronotum (except hind angles), and elytral intervals 4, 6 and 8 (Fig. 122,133). Distinguished easily from members of remaining species by scattered punctures (30 to 120 microns apart) on elytral intervals 4, 6 and 8 (Fig 122). and by much sparser punctures (10 to 120 microns apart) on pleura and laterally on thoracic and abdominal sterna.

Adults. Description.- Upper surface dark brassy-green or copper in most boreal regions and along the Rockies, or much darker, even black, elsewhere; pits purple and postero-lateral angles of pronotum and impression on head in most specimens bright green metallic; ventral surface black or black with brassy-green hue; legs reddish brown in most specimens from northeastern United States and adjacent areas of Canada or dark brown; femur with green metallic hue, and dorsal surface of tibia and tarsomeres purple.

Mentum tooth moderately emarginate: emargination about 0.5 length of tooth. Pronotum of most specimens with main discal impression only (submedial one in very few specimens). Prosternal process with one to four accessory setae in about 50% of specimens. Most punctures on antero-medial surface of metasternum with setae. Abdominal sternum 7 with few punctures; sterna 5 and 6 each with 15 to 25 accessory setae, sternum 7 with about 20 accessory setae in males and five to 15 accessory setae in females. Setigerous punctures of elytral pits clearly outlined; lateral ridges of pits clearly fused anteriorly and posteriorly (Fig. 133), in form of rings; pits with eight to 10 punctures near suture. Mirrors distinct on intervals 3 and 5, mirrors little contrasted especially on dark specimens. Femur of foreleg and midleg with about 50 setae, and of hind leg with seven to 10 setae. Tibia of midleg of males with sharp apico-internal projection between spurs (Fig. 150); tibia of foreleg with about 20 setae (excluding setae of fringe), and of midleg and hind leg with about 55 to 60 setae. Hind coxa with punctures on external 0.5 and with only three to seven accessory setae near internal margin.

Integument sculpture. Punctures moderately small dorsally (20 to 25 microns in size), and moderate ventrally (25 to 30 microns). Punctures on dorsal surface scattered: 20 to 75 microns apart on side of pronotum, and 30 to 120 microns apart on intervals 4, 6 and 8 (Fig. 122); ventrally punctures denser (five to 60 microns apart); 20 to 180 microns apart on prosternum and laterally on abdominal sterna five to 100 microns apart; punctures on coxae 30 to 80 microns apart. Punctures sharply outlined on dorsal surface over 30 to 50% of circumference of punctures and on pleura and laterally on thoracic and abdominal sterna over 50 to 70% of punctures.

Male genitalia. Apex of median lobe in dorsal view moderately extended beyond apex of internal sac, apex wide (40 to 60 microns thick) and strongly twisted (Fig. 50a); in lateral view apex narrow, slightly spatulate and slightly bent ventrally (Fig 50b).

Measurements and proportions.- I analyzed 20 samples. See Tables 12 to 23 for 12 of these samples that illustrate the pattern of variation.

Variation. The most easily observed variation was color of the dorsal surface (Fig. 162). In northeastern United States and adjacent Canada adults are small, black-bodied and reddish legged. In western Canada individuals are dark green, large-bodied and black-legged. This form extends southward along the Rocky Mountains to Colorado and eastern Arizona. However, many smoother and somewhat duller specimens are mixed among a majority of more typical bright specimens in Utah and Colorado. The Arizona sample includes only duller individuals. The western Canadian form extends into British Columbia and eastern Alaska. In westernmost United States and adjacent Canada (i.e. west of the continental divide), specimens are nearly black, those of the Pacific coast are mostly black. These data suggest a rather distinct eastern form, a clinal change along the Rocky Mountains from the boreal form to the duller more southern form, and a slightly differentiated Great Basin and Pacific coast form.

An independent study of body proportions indicates more clearly this same pattern. I carefully chose 20 samples across the range of this species. The most consistent differences were between eastern United States (including

Table 12. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Phelps Botanical Garden, White Mountains Arizona.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.1	2.00	0.086	0.026	2.9
PW	2.0-2.4	2.21	0.129	0.038	3.9
EL	4.7-5.2	4.98	0.231	0.069	3.1
EW	1.7-1.9	1.88	0.108	0.032	4.1
HW	2.0-2.2	2.16	0.106	0.032	3.3
B. Proportions.					
PL/PW	0.865-0.932	0.902	0.028	0.008	2.0
PL/EL	0.388-0.412	0.401	0.011	0.003	1.8
PL/EW	1.060-1.180	1.120	0.052	0.015	3.1
PL/HW	0.889-0.963	0.926	0.025	0.008	1.8
PW/EL	0.431-0.471	0.445	0.014	0.004	2.0
PW/EW	1.180-1.330	1.240	0.055	0.016	3.0
PW/HW	0.989-1.080	1.030	0.035	0.010	2.3
EL/EW	2.690-2.910	2.800	0.091	0.027	2.2
EL/HW	2.230-2.390	2.310	0.075	0.022	2.2
EW/HW	0.782-0.874	0.825	0.039	0.012	3.2

Table 13. Descriptive statistics for E. *clairvillei* based on 10 males and 10 females from Rocky Mountain National Park, Colorado and neighbouring localities.

Character	Range	Mean	1.5SD	2SE	CV(%)
A. Measurements in mm.					
PL	1.8-2.2	2.01	0.186	0.044	4.8
PW	2.0-2.4	2.17	0.173	0.052	5.3
EL	4.5-5.6	4.98	0.392	0.116	5.2
EW	1.6-2.0	1.77	0.164	0.049	6.2
HW	2.1-2.4	2.19	0.148	0.044	4.5
B. Proportions.					
PL/PW	0.875-0.976	0.924	0.051	0.015	3.7
PL/EL	0.375-0.432	0.404	0.017	0.005	2.9
PL/EW	1.050-1.210	1.130	0.058	0.017	3.4
PL/HW	0.869-0.968	0.915	0.041	0.012	3.0
PW/EL	0.408-0.465	0.437	0.024	0.007	3.6
PW/EW	1.140-1.320	1.230	0.081	0.024	4.4
PW/HW	0.932-1.060	0.991	0.048	0.014	3.2
EL/EW	2.680-2.940	2.810	0.094	0.028	2.2
EL/HW	2.140-2.370	2.270	0.103	0.031	3.0
EW/HW	0.771-0.860	0.807	0.040	0.012	3.3

Table 14. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from southcentral British Columbia: Wardner, Wyndel, Osoyous, and Creston.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.1	1.97	0.138	0.041	4.7
PW	2.0-2.5	2.14	0.165	0.049	5.2
EL	4.5-5.5	4.90	0.315	0.094	4.3
EW	1.6-2.1	1.75	0.149	0.044	5.6
HW	2.0-2.5	2.21	0.158	0.047	4.8
B. Proportions.					
PL/PW	0.869-0.954	0.920	0.036	0.011	2.6
PL/EL	0.378-0.417	0.402	0.018	0.005	3.0
PL/EW	1.030-1.200	1.120	0.072	0.021	4.3
PL/HW	0.841-0.938	0.892	0.037	0.011	2.7
PW/EL	0.420-0.450	0.437	0.012	0.004	1.9
PW/EW	1.140-1.300	1.200	0.061	0.018	3.3
PW/HW	0.932-1.010	0.970	0.031	0.009	2.1
EL/EW	2.650-2.970	2.800	0.120	0.036	2.9
EL/HW	2.150-2.280	2.220	0.057	0.017	1.7
EW/HW	0.750-0.838	0.795	0.036	0.011	3.0

Table 15. Descriptive statistics for *E. clairvillei* based on eight males and three females from Terrace, British Columbia.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.1	1.97	0.077	0.031	2.6
PW	2.0-2.2	2.12	0.118	0.047	3.7
EL	4.7-5.1	4.97	0.205	0.082	2.7
EW	1.6-1.8	1.75	0.111	0.045	4.2
HW	2.1-2.3	2.20	0.074	0.030	2.3
B. Proportions.					
PL/PW	0.889-0.988	0.931	0.044	0.018	3.2
PL/EL	0.385-0.411	0.397	0.013	0.005	2.2
PL/EW	1.100-1.180	1.130	0.044	0.018	2.6
PL/HW	0.885-0.922	0.896	0.018	0.007	1.3
PW/EL	0.400-0.448	0.427	0.020	0.008	3.1
PW/EW	1.130-1.260	1.210	0.070	0.028	3.8
PW/HW	0.909-1.000	0.963	0.040	0.016	2.7
EL/EW	2.770-3.000	2.840	0.104	0.042	2.4
EL/HW	2.180-2.300	2.260	0.063	0.025	1.8
EW/HW	0.750-0.830	0.794	0.035	0.014	3.0

Table 16. Descriptive statistics for *E. clairvillei* based on 10 males and nine females from Seattle, Washington.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.0	1.98	0.100	0.030	3.4
PW	2.0-2.3	2.10	0.125	0.038	3.9
EL	4.6-5.1	4.80	0.230	0.070	3.2
EW	1.6-1.8	1.71	0.108	0.033	4.2
HW	2.0-2.3	2.11	0.124	0.038	3.9
B. Proportions.					
PL/PW	0.881-0.964	0.919	0.041	0.012	3.0
PL/EL	0.384-0.421	0.404	0.019	0.006	3.1
PL/EW	1.030-1.200	1.130	0.069	0.021	4.1
PL/HW	0.872-0.976	0.915	0.038	0.012	2.8
PW/EL	0.413-0.468	0.439	0.019	0.006	2.9
PW/EW	1.160-1.340	1.230	0.060	0.018	3.3
PW/HW	0.954-1.050	0.995	0.034	0.010	2.2
EL/EW	2.600-2.950	2.810	0.117	0.036	2.8
EL/HW	2.180-2.390	2.270	0.088	0.027	2.6
EW/HW	0.768-0.849	0.809	0.036	0.011	3.0

Table 17. Descriptive statistics for *E. clairvillei* based on seven males and 10 females from Williams Lake, British Columbia.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	2.0-2.1	2.05	0.056	0.018	1.8
PW	2.1-2.4	2.20	0.105	0.034	3.1
EL	5.0-5.6	5.25	0.274	0.088	3.5
EW	1.8-2.0	1.87	0.105	0.034	3.7
HW	2.2-2.3	2.25	0.070	0.023	2.1
B. Proportions.					
PL/PW	0.874-0.976	0.917	0.035	0.011	2.6
PL/EL	0.375-0.407	0.392	0.015	0.005	2.5
PL/EW	1.050-1.150	1.100	0.051	0.016	3.1
PL/HW	0.860-0.955	0.911	0.030	0.010	2.2
PW/EL	0.398-0.452	0.428	0.022	0.007	3.4
PW/EW	1.100-1.280	1.190	0.070	0.022	3.9
PW/HW	0.933-1.050	0.944	0.045	0.015	3.0
EL/EW	2.700-2.880	2.790	0.062	0.020	1.5
EL/HW	2.180-2.490	2.320	0.119	0.038	3.4
EW/HW	0.763-0.889	0.833	0.047	0.015	3.8

Table 18. Descriptive statistics for *E. clairvillei* based on nine males and seven females from eastern Alaska: Circle; Alaska Hwy: mi. 1249, 1442; Richardson Hwy: mi. 148, 285.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.1	2.01	0.100	0.034	3.3
PW	2.0-2.4	2.17	0.155	0.053	4.8
EL	4.8-5.5	5.10	0.333	0.114	4.3
EW	1.7-1.9	1.83	0.118	0.041	4.3
HW	2.0-2.3	2.15	0.118	0.041	3.7
B. Proportions.					
PL/PW	0.874-0.988	0.928	0.053	0.018	3.3
PL/EL	0.378-0.417	0.395	0.018	0.006	3.1
PL/EW	1.050-1.180	1.100	0.053	0.018	3.2
PL/HW	0.901-0.964	0.934	0.027	0.009	1.9
PW/EL	0.405-0.453	0.426	0.023	0.008	3.7
PW/EW	1.130-1.260	1.180	0.060	0.020	3.4
PW/HW	0.966-1.060	1.010	0.046	0.016	3.0
EL/EW	2.700-2.860	2.780	0.075	0.026	1.8
EL/HW	2.290-2.470	2.370	0.077	0.027	2.2
EW/HW	0.814-0.880	0.853	0.033	0.011	2.6

Table 19. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Fawcett, Alberta.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	2.0-2.1	2.04	0.066	0.020	2.2
PW	2.1-2.3	2.21	0.114	0.034	3.4
EL	4.8-5.5	5.15	0.273	0.081	3.5
EW	1.7-2.0	1.88	0.094	0.028	3.3
HW	2.1-2.3	2.24	0.093	0.028	2.8
B. Proportions.					
PL/PW	0.892-0.965	0.928	0.034	0.010	2.5
PL/EL	0.366-0.421	0.397	0.023	0.007	3.8
PL/EW	1.020-1.180	1.090	0.060	0.018	3.7
PL/HW	0.872-0.943	0.913	0.029	0.009	2.1
PW/EL	0.389-0.450	0.428	0.022	0.077	3.5
PW/EW	1.090-1.240	1.180	0.062	0.018	3.5
PW/HW	0.944-1.020	0.984	0.031	0.009	2.1
EL/EW	2.660-2.880	2.750	0.095	0.028	2.3
EL/HW	2.170-2.440	2.300	0.103	0.031	3.0
EW/HW	0.782-0.882	0.838	0.038	0.011	3.0

Table 20. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Riverton, Manitoba.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.2	2.01	0.109	0.032	3.6
PW	1.9-2.3	2.12	0.138	0.041	4.4
EL	4.6-5.2	4.91	0.269	0.080	3.7
EW	1.6-1.9	1.76	0.114	0.034	4.3
HW	2.1-2.4	2.24	0.100	0.030	3.0
B. Proportions.					
PL/PW	0.899-0.988	0.950	0.038	0.011	2.6
PL/EL	0.393-0.433	0.411	0.017	0.005	2.8
PL/EW	1.070-1.220	1.140	0.071	0.021	4.1
PL/HW	0.870-0.933	0.898	0.025	0.007	1.8
PW/EL	0.406-0.448	0.432	0.015	0.005	2.4
PW/EW	1.130-1.280	1.200	0.060	0.018	3.3
PW/HW	0.907-0.989	0.946	0.035	0.010	2.4
EL/EW	2.690-2.900	2.780	0.096	0.028	2.3
EL/HW	2.110-2.310	2.190	0.089	0.027	2.7
EW/HW	0.742-0.844	0.787	0.041	0.012	3.5

Table 21. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from northern Michigan: White Fish Point; Huron Mountains; Escabana; Naubinway; St. Ignace.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.1	2.01	0.078	0.023	2.6
PW	2.0-2.2	2.12	0.100	0.030	3.1
EL	4.6-5.1	4.85	0.229	0.068	3.1
EW	1.6-1.9	1.75	0.101	0.030	3.9
HW	2.1-2.4	2.24	0.091	0.027	2.7
B. Proportions.					
PL/PW	0.909-1.000	0.949	0.039	0.012	2.7
PL/EL	0.396-0.446	0.415	0.019	0.006	3.1
PL/EW	1.050-1.220	1.150	0.053	0.016	3.1
PL/HW	0.857-0.933	0.889	0.029	0.009	2.2
PW/EL	0.426-0.452	0.437	0.011	0.003	1.7
PW/EW	1.160-1.280	1.210	0.045	0.014	2.5
PW/HW	0.902-0.967	0.937	0.025	0.007	1.8
EL/EW	2.660-2.860	2.770	0.090	0.027	2.2
EL/HW	2.060-2.240	2.140	0.075	0.022	2.3
EW/HW	0.732-0.817	0.775	0.030	9.009	2.6

Table 22. Descriptive statistics for *E. clairvillei* based on 10 males and 10 females from Ridgewood, New York.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.8-2.1	1.98	0.159	0.036	2.0
PW	2.0-2.2	2.06	0.089	0.026	2.9
EL	4.3-4.9	4.63	0.232	0.069	3.3
EW	1.5-1.8	1.70	0.101	0.030	4.0
HW	2.0-2.3	2.25	0.111	0.033	3.3
B. Proportions.					
PL/PW	0.931-1.000	0.963	0.022	0.066	1.5
PL/EL	0.417-0.453	0.428	0.015	0.004	2.3
PL/EW	1.110-1.260	1.170	0.050	0.015	2.8
PL/HW	0.860-0.951	0.882	0.032	0.009	2.4
PW/EL	0.428-0.465	0.445	0.016	0.005	2.4
PW/EW	1.150-1.290	1.210	0.049	0.015	2.7
PW/HW	0.889-1.000	0.916	0.038	0.011	2.8
EL/EW	2.640-2.830	2.730	0.097	0.029	2.4
EL/HW	1.930-2.250	2.060	0.107	0.032	3.4
EW/HW	0.697-0.827	0.755	0.046	0.024	4.1

Table 23. Descriptive statistics for *E. clairvillei* based on four males and three females from Newfoundland (Cow Head; Harrys Harbour; Springdale) and Labrador (Forteau).

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.9-2.0	1.99	0.108	0.054	3.6
PW	2.0-2.2	2.13	0.107	0.054	3.4
EL	4.7-5.2	4.96	0.219	0.110	2.9
EW	1.7-1.8	1.79	0.028	0.014	1.0
HW	2.1-2.3	2.22	0.131	0.066	3.9
B. Proportions.					
PL/PW	0.904-0.953	0.933	0.026	0.013	1.9
PL/EL	0.387-0.418	0.401	0.015	0.007	2.4
PL/EW	1.040-1.140	1.110	0.053	0.026	3.2
PL/HW	0.862-0.921	0.895	0.043	0.022	3.2
PW/EL	0.420-0.454	0.430	0.017	0.008	2.6
PW/EW	1.150-1.240	1.190	0.050	0.025	2.8
PW/HW	0.913-1.000	0.954	0.048	0.024	3.3
EL/EW	2.690-2.890	2.770	0.100	0.050	2.4
EL/HW	2.150-2.340	2.230	0.098	0.049	2.9
EW/HW	0.766-0.893	0.807	0.039	0.020	3.2

adjacent Canada) and the remaining populations. At least most eastern samples show significantly larger means for the following ratios: PL/PW, PL/EL, PL/HW, PW/HW, EL/HW and EW/HW, and significantly smaller means for PL/EW (*i.e.* eastern specimens have relatively narrower heads, longer pronota and wider elytra) (Fig. 163 and 164). However, some of these differences are less expressed northward into southern Manitoba, northern Michigan and on the north shore of the St. Lawrence River (St. Fidele). The sample from Riverton, Manitoba is intermediate between eastern and western forms. Surprisingly, specimens from Newfoundland are typical of the western form. Thus the eastern form intergrades with the western form in Manitoba and almost certainly so across northern Ontario and Quebec, although I have only small samples from that area. If so, the Newfoundland population might not be as isolated as first suggested. Interpopulational differences in the western form are generally inconsistent. Samples from southern boreal regions (Williams Lake, British Columbia; Cypress Hills, Alberta; Churchill, Manitoba; and Newfoundland) are similar to those from Colorado, the Great Basin (including the sample from southcentral British Columbia). The sample from eastern Arizona is most similar to the Colorado sample but is consistently different from this and samples from localities in the Great Basin in having a significantly larger ratio PW/HW. The only other significantly different populations are the adjacent samples from southcentral

British Columbia and Terrace, British Columbia to boreal British Columbia. These two samples are slightly (significantly smaller means for ratio PW/HW and EL/HW) or not different from samples south of these localities, but are consistently different from more northern boreal samples with significantly smaller means for ratios: PW/HW, EL/HW and EW/HW (i.e. the head is relatively wider). These results suggest character displacement between the boreal form and the form south of it. However, data on variation suggest gene flow between the Great Basin and Colorado populations and the boreal regions; thus samples from southcentral British Columbia and Terrace are connected probably genetically to the boreal region by the Great Basin-Rocky Mountain arc. Boreal populations probably are connected by gene flow with populations from the Great Basin, Pacific coast, Rocky Mountains, and eastern populations. However, samples from western North America (eastern Alaska, northernmost British Columbia, southern Yukon, and northcentral Alberta) show significantly larger means for ratio EW/HW. Most samples also show significantly larger means for ratios PW/HW, EL/HW, and PW/EW. These differences are most pronounced in eastern Alaska. The data suggest gene flow between northwestern populations and other southern and eastern boreal populations.

In summary, I can recognize a boreal, western (Great Basin and Pacific coast), and a New England (including adjacent Canada) form; but gene flow is apparently uninterrupted between them. Therefore I do not consider it necessary to recognize subspecies.

First Instar Larvae. Diagnostic combination.- Very similar to members of E. cupreus but meshes of microsculpture more widespread dorso-laterally on parietale, but more narrowly expanded ventrally near neck; pointed sculpture on 10% of dorso-lateral surface, and 2% of latero-ventral surface. Distinguished from remaining species by lack of sculpture on disc of pronotum, and reduced amount of pointed sculpture ventrally on thoracic membrane (15% of surface).

First Instar Larvae. Description.- Seta MP of frontale small. Setae DMM-A and DMP-A of parietale medium; meshes of microsculpture on 20% of surface and 2% of ventro-lateral surface. Setae AII-E of pronotum medium; sculpture absent from disc. Meshes of microsculpture on 20% of mesonotal disc and 30% of metanotal disc; pointed sculpture near suture on 7% of disc of mesonotum and 15% of disc of matanotum, and laterally on 5% of both nota, absent from posterior bands of these nota. Setae AII and AIM of terga 1 to 8 medium in size. Pointed sculpture of urogomphus of tergum 9 clearly outlined, extended on abdominal sternite 10, more restricted on ventro-thoracic surface of membrane (20% of surface), not extended to proepisternum, and slightly more expanded on ventro-abdominal surface around hypopleuron 1 to 8.

Second Instar Larvae. Diagnostic combination.- Very similar to members of E. cupreus but meshes of microsculpture on 10% of disc of pronotum and pointed sculpture on abdominal membrane expanded ventrally toward sternites 2 to 7. Distinct from remaining members by presence of pointed sculpture near suture on 2% of disc of mesonotum and 10% of disc of metanotum, and on 10% of anterior band of tergum 9.

Second Instar Larvae. Description.- Pointed sculpture dorso-laterally on 15% of parietale surface, and absent ventro-laterally. Major accessory setae on pronotal epipleuron medium-small; meshes of microsculpture on 10% of disc of pronotum, on 40% of mesonotal and metanotal surface; pointed sculpture near suture on 2% of disc of mesonotum and 10% of disc of metanotum, and laterally on 15% of both nota. Mesepisternum and metepisternum without sculpture. Tergum 2 and following with sculpture on surface; urogomphus of tergum 9 with scale-like single-pointed sculpture; pointed sculpture on 10% of anterior band of tergum 9. Sculpture on tergum 10 multi-pointed. Pointed sculpture of membrane on ventral side of abdomen expanded to sternite and behind poststernites.

Third Instar Larvae. Diagnostic combination.- Very similar to specimens of E. cupreus but microsculpture less extended on terga 1 to 5. Distinct from other members by lack of microsculpture from disc of pronotum, by presence of pointed sculpture laterally on disc of mesonotum and metanotum, and on 60% of anterior band of tergum 9.

Third Instar Larvae. Description.- Pronotum without microsculpture. Meshes of microsculpture on 40% of disc of mesonotum; pointed sculpture present on 10% of surface near suture and laterally. Metathorax as mesothorax. Pointed sculpture on 5% or more of anterior band of terga 1 to 8, on 60% of anterior band of tergum 9, and on 5% or more of posterior band of terga 1 to 8. Sculpture of urogomphus of tergum 9 with scale-like single-pointed sculpture; terga 1 to 5 with restricted microsculpture on entire surface. Abdominal sternite 9 with six accessory setae. Sculpture of membrane expanded on ventral side of abdomen.

Distribution.- The range of this species extends through all of cold temperate and boreal regions of North America, from Alaska to Newfoundland as far north as treeline, and as far south as northern New England in the east and northern California in the west. Along the Rocky Mountains the range of *E. clairvillei* extends south to Colorado and the White Mountains of eastern Arizona (Fig. 160). I studied more than 1500 adults and dissected more than 100 males. I examined seven first instar, five second instar and four third instar larvae from George Lake, Alberta.

Collecting notes.- Members of this species live on soft wet organic mud in the shade of sedges (*Carex* and

Amblystegium vegetation), or taller vegetation (*Typha* and *Alnus*), or under forest canopy. Females oviposit from mid-May until late July. Immatures are common in June, and larvae of all three instars can be found together in July. In the field pupae are found in rotten logs. Though development is rapid, teneral adults do not appear until the end of July, thus probably emergence is synchronized. Teneral adults as well as older adults are seen until the end of September. Thereafter most adults are found in forest litter where soil is naturally well drained, or under bark of old logs that are well above flood level. Only adults overwinter. During the first half of May adults return to the marshes. Adults are diurnal and can live for at least two summers (*i.e.* many females are found in early May with large *corpora lutea*). Larvae live in the same general habitat as the adults but are mostly inside soil. Adults are opportunist feeders, as observed in the field and the laboratory, where they feed on any soft-bodied animals. I have not observed predatory behaviour among adults, but larvae attack small arthropods of any type, including each other in laboratory conditions despite abundance of food.

Geographical affinities.- This species is sympatric with *E. olivaceus* and perhaps in northeastern California with *E. laevigatus*, both members of the *cupreus* group. It is also sympatric with *E. fuliginosus* and *E. cicatricosus* in eastern North America.

Relationships.- It is closely related to *E. olivaceus* and *E. laevigatus* as shown by the shared derived restricted microsculpture on the dorsal surface and the elytral pit ridges that are fused anteriorly and posteriorly. However, it is ancestral to both above species as shown by ventral punctures, larger dorsal punctures, and presence of setae on apex of prosternal intercoxal process.

3.5.3.13. *Elaphrus olivaceus* LeConte

Elaphrus olivaceus LeConte 1863: 1. *Type locality* - Catskill Mountains, New York; type not seen by me or Lindroth; one specimen in LeConte's collection from Marquette, Michigan at the Museum of Comparative Zoology, Cambridge, Massachussetts, Lindroth 1961: 113.

Adults. *Diagnostic combination*.- Adults of this species are immediately distinguished from any other member of this group by the brown antennomeres 1 to 3, the very fine, dense and widespread punctures on disc of metasternum and of hind coxae. Otherwise, adults are very similar dorsally to adults of *E. pyrenaeus* of the *uliginosus* group.

Adults. *Description*.- Upper surface green (bright emerald to olive), blue green, dark brown olive, or reddish brown except for purple pits; ventral surface dark green-gold metallic or copper metallic; legs, palps and antennomeres 1 to 3 rufous, femur with green or copper hue, apex of tibia and tarsomeres green or copper metallic on dorsal surface.

Mentum tooth very slightly emarginate: emargination 0.2 to 0.25 length of tooth. Pronotum with two discal impressions. Prosternal process without accessory setae. Metasternum densely punctate antero-medially, few punctures with setae (about 20%). Abdominal sterna 3 and 4 each with 10 to 20 accessory setae, sterna 5, 6 and 7 each without or with one or two accessory setae (Fig. 139). Setigerous punctures on elytra clearly outlined. Elytral pits near suture with eight to 15 punctures; lateral ridges narrow and apparently fused anteriorly and posteriorly--especially those near suture (Fig. 134). Mirrors indistinctly outlined on intervals 3 and 5, and very slightly contrasted against microsculpture-free intervals 4, 6 and 8.

Hind coxae densely punctate over surface and two to five accessory setae along internal margin. Femur of foreleg with about 20 setae. Tibia of midleg of males without sharp apico-internal projection between spurs; tibia of foreleg with about 20 setae and of midleg and hind leg with about 60 setae.

Integument sculpture. Punctures fine (15 to 20 microns in size) on head, pronotum and elytral intervals 4, 6 and 8 (Fig. 123); moderate (25 to 30 microns) on pleura, and laterally on thoracic and abdominal sterna, and on coxae; very dense (10 to 20 microns apart) on head, pronotum (side), and elytral intervals 4, 6 and 8, on pleura and abdominal sterna; moderately dense (5 to 50 microns apart) on thoracic sterna and coxae. Punctures sharply outlined on 30% of circumference on elytra and clypeus; sharply outlined on 50 to 70% of circumference on head, pronotum, pleura and laterally on thoracic and abdominal sterna.

Meshes of microsculpture absent from head, pronotum (except postero-lateral angles and laterally), and elytra (Fig. 134) (except in pits and near shoulder). Alveolae flat laterally on pronotum, near shoulder, on thoracic sterna, on propleuron and mesopleuron; convex or subconvex on metapleuron, abdomen, postero-lateral impressions of pronotum and elytral pits.

Male genitalia. Apex of median lobe in dorsal view very shortly extended in front of internal sac, very sharp (20 microns wide) and not twisted (Fig. 51a); in lateral view apex narrow (Fig. 51b).

Measurements and proportions.- I studied seven samples of which data for the five most pertinent for understanding of geographical variation are presented in Tables 24 to 28.

Variation.- Adults from Colorado, Alberta and eastern North America, at first glance, are similar. However, populations from these regions differ in the number and presence of different color forms (Fig. 165). In coastal New England there are two color forms: blue green and olive. In interior New England (*e.g.* Green Mountains, Vermont and Adirondack Mountains, New York) these two forms co-exist with a third dark brown form with green punctures. This last form is not discrete because specimens between the dark

Table 24. Descriptive statistics for E. *olivaceus* based on two males and four females from Central Colorado: Fairplay, Santa Maria, Plum Creek, Bellevue.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.6-1.8	1.72	0.087	0.047	3.4
PW	1.8-1.9	1.85	0.050	0.027	1.8
EL	3.8-4.2	4.08	0.215	0.117	3.5
EW	1.4-1.6	1.49	0.117	0.064	5.2
HW	1.9-1.9	1.92	0.050	0.027	1.7
B. Proportions.					
PL/PW	0.904-0.973	0.928	0.027	0.020	2.7
PL/EL	0.411-0.429	0.422	0.011	0.006	1.7
PL/EW	1.110-1.200	1.150	0.058	0.031	3.3
PL/HW	0.846-0.936	0.896	0.045	0.024	3.3
PW/EL	0.441-0.474	0.455	0.017	0.009	2.4
PW/EW	1.190-1.130	1.240	0.081	0.044	4.3
PW/HW	0.936-1.000	0.965	0.031	0.017	2.2
EL/EW	2.650-2.810	2.730	0.102	0.055	2.5
EL/HW	1.970-2.210	2.120	0.128	0.069	4.0
EW/HW	0.705-0.813	0.779	0.064	0.035	5.5

Table 25. Descriptive statistics for *E. olivaceus* based on 10 males and 10 females from Flatbush, Alberta.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-2.0	1.81	0.108	0.032	4.0
PW	1.7-2.0	1.83	0.111	0.033	4.0
EL	4.0-4.6	4.23	0.266	0.079	4.2
EW	1.4-1.7	1.55	0.134	0.040	5.7
HW	1.8-2.1	1.93	0.091	0.027	3.1
B. Proportions.					
PL/PW	0.946-1.040	0.993	0.047	0.014	3.2
PL/EL	0.403-0.455	0.430	0.023	0.007	3.6
PL/EW	1.070-1.290	1.170	0.080	0.024	4.6
PL/HW	0.900-0.974	0.937	0.034	0.010	2.4
PW/EL	0.407-0.462	0.433	0.022	0.007	3.4
PW/EW	1.090-1.260	1.180	0.073	0.022	4.2
PW/HW	0.909-1.000	0.944	0.073	0.010	2.4
EL/EW	2.580-2.860	2.720	0.100	0.030	2.4
EL/HW	2.100-2.290	2.180	0.083	0.025	2.5
EW/HW	0.747-0.857	0.813	0.046	0.014	3.8

Table 26. Descriptive statistics for *E. olivaceus* based on 11 males and nine females from Medicine Hat, Alberta.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-2.0	1.82	0.145	0.043	5.3
PW	1.7-2.0	1.87	0.144	0.043	5.1
EL	3.6-4.6	4.17	0.387	0.115	6.2
EW	1.3-1.7	1.53	0.159	0.047	6.9
HW	1.7-2.1	1.96	0.126	0.037	4.3
B. Proportions.					
PL/PW	0.921-1.030	0.9	0.034	0.010	2.3
PL/EL	0.415-0.479	0.439	0.022	0.006	3.3
PL/EW	1.120-1.270	1.190	0.061	0.018	3.4
PL/HW	0.875-0.964	0.929	0.039	0.011	2.8
PW/EL	0.425-0.500	0.450	0.026	0.008	3.8
PW/EW	1.150-1.330	1.220	0.066	0.020	3.6
PW/HW	0.913-1.000	0.951	0.042	0.013	3.0
EL/EW	2.640-2.830	2.710	0.076	0.023	1.9
EL/HW	1.900-2.260	2.120	0.115	0.034	3.6
EW/HW	0.714-0.840	0.781	0.044	0.013	3.7

Table 27. Descriptive statistics for E. *olivaceus* based on nine males and 10 females from southern Manitoba: Aweme; Victoria Beach; Rosebank; Brandon; Pelican Lake.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.7-1.9	1.80	0.102	0.031	3.8
PW	1.6-2.0	1.82	0.136	0.042	5.1
EL	3.7-4.6	4.09	0.350	0.110	5.6
EW	1.3-1.7	1.51	0.148	0.045	6.5
HW	1.8-2.1	1.97	0.111	0.034	3.8
B. Proportions.					
PL/PW	0.959-1.080	0.991	0.040	0.012	2.7
PL/EL	0.415-0.466	0.441	0.023	0.007	3.4
PL/EW	1.110-1.300	1.190	0.082	0.025	4.6
PL/HW	0.872-0.945	0.912	0.029	0.009	2.1
PW/EL	0.420-0.469	0.444	0.020	0.006	3.0
PW/EW	1.120-1.300	1.200	0.062	0.019	3.4
PW/HW	0.877-0.964	0.920	0.039	0.012	2.8
EL/EW	2.580-2.840	2.710	0.100	0.030	2.5
EL/HW	1.930-2.220	2.070	0.112	0.034	3.6
EW/HW	0.723-0.819	0.766	0.047	0.014	4.1

Table 28. Descriptive statistics for *E. olivaceus* based on 10 males and 10 females from Penobsquis River, New Brunswick.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.6-1.9	1.77	0.115	0.034	4.3
PW	1.6-1.9	1.77	0.115	0.034	4.3
EL	3.6-4.3	4.02	0.334	0.110	5.5
EW	1.3-1.6	1.52	0.136	0.040	6.0
HW	1.8-2.1	1.93	0.118	0.035	4.1
B. Proportions.					
PL/PW	0.944-1.010	0.990	0.030	0.009	2.0
PL/EL	0.424-0.468	0.442	0.019	0.006	2.9
PL/EW	1.110-1.240	1.170	0.053	0.016	3.0
PL/HW	0.887-0.947	0.916	0.025	0.007	1.8
PW/EL	0.425-0.480	0.447	0.023	0.007	3.4
PW/EW	1.120-1.270	1.180	0.067	0.020	3.8
PW/HW	0.892-0.973	0.926	0.031	0.009	2.3
EL/EW	2.530-2.750	2.650	0.082	0.024	2.1
EL/HW	1.950-2.180	2.070	0.087	0.026	2.8
EW/HW	0.741-0.833	0.783	0.035	0.010	3.0

brown-olive form and the olive form exist. In boreal Quebec, on the north shore of the St. Lawrence river (e.g. St. Fidele), the brown form with golden punctures is clearly distinct. From this last locality to Medicine Hat, Alberta, I have seen specimens of these three color forms. However, background color changes from the dark olive-brown to red-brown in Medicine Hat; but punctures are golden. Thus, this third color form becomes more distinct westward. In central and northern Alberta I collected only two color forms: olive and red-brown. This last form has copper punctures. My samples from Newfoundland and Colorado are too small to determine range of color forms. From Newfoundland I have two forms: olive and blue-green, and from Colorado only olive specimens. These results suggest a cline from east to west in the formation and differentiation of a third color form. Three forms exist from eastern Canada to Medicine Hat, Alberta, but only two in central Alberta. Thus there is suggestion of a break in gene flow, but the reddish-brown form, though very distinct, is nevertheless most similar to the brown form from Medicine Hat. Therefore, gene flow might still exist in areas of either the Rocky Mountain foothills or the boreal regions of Saskatchewan and Manitoba that have not been adequately sampled.

In an attempt to clarify this problem I studied variation in body proportions by means of carefully chosen samples from across the range of this species. The results confirmed and completed the general picture presented above.

The Colorado sample showed lower mean values for ratios PL/PW and PL/EL than other samples (i.e. the pronotum is relatively shorter) (Fig. 166). This sample is most similar to the one from central Alberta and most different from the sample from Medicine Hat, Alberta. The central Alberta sample is consistently different from all more eastern samples with its significantly larger mean for ratio EL/HW, it also differs significantly from most eastern samples in its mean for each of the following ratios: PL/HW, PW/HW and EW/HW (i.e. the head is relatively narrower) (Fig. 167). The northern Alberta sample is most similar to the Medicine Hat sample and increasingly different from samples eastward. The sample from Medicine Hat, Alberta is consistently different from other eastern samples in having a significantly larger mean for ratio PW/HW. The most similar sample east of this locality is that from southern Manitoba; and the most different samples are those from New Brunswick and Newfoundland. However, because the differences are not consistent, the data suggests some gene flow between populations in Medicine Hat and eastern North America. Samples from southern Manitoba to Newfoundland are not different or not consistently different.

The data suggests basically three forms: one from Colorado, another from northern Alberta and a third extending from Medicine Hat, Alberta eastward. However, the Medicine Hat sample is both most proximate and most similar to the Colorado and northern Alberta sample. Although more specimens are needed from the Rocky Mountain area and the northern Prairie provinces, the data suggest that gene flow takes place among these populations. Therefore, I do not consider it necessary to recognize subspecies.

Derivation of specific epithet.- From latin "olive" referring to color of the dorsum of the common color form.

First Instar Larvae. Diagnostic combination.- Similar to members of E. laevigatus but distinguished by more restricted pointed sculpture on parietale (5% of dorsal and 3% of ventral surfaces), and distinct from remaining members by presence of meshes of microsculpture on 5% of disc of pronotum, the very extended pointed sculpture on ventral surface of thoracic membrane (45% of surface), the very fine pointed sculpture of urogomphi and the restricted pointed sculpture to the base of abdominal sternite 10.

First Instar Larvae. Description.- Seta MP of frontale very small. Parietal setae A and DMP-A small to medium-small. Meshes of microsculpture expanded on baso-lateral surface (50% of parietal dorsal surface), and along ventro-lateral surface; pointed sculpture near neck on 5% of dorsal surface and 3% of ventral surface. Seta AII-E of pronotum medium; meshes of microsculpture on 5% of disc, on 40% of disc of mesonotum; pointed sculpture present near suture on 20% of disc and laterally on 5% of disc, and sculpture absent from posterior band. Metanotum as mesonotum. Setae AII and AIM of terga 1 to 8 medium sized. Pointed sculpture on abdominal sternite 10 restricted to base only; on membrane expanded ventrally; on thorax over 40% of surface and sculpture extended clearly toward proepisternum; on abdomen extended around hypopleuron and more sparsely extended toward abdominal sternites 2 to 7.

Second Instar Larvae. Diagnostic combination.- Similar to members of E. laevigatus but pointed sculpture more restricted on parietal dorsal surface to 15%, and to 3% of ventral surface, and major accessory setae on pronotal epipleuron medium. They are distinct from remaining members by lack of pointed sculpture on mesonotum and metanotum, and on the anterior band of tergum 9.

Second Instar Larvae. Description.- Pointed sculpture of parietale on 15% of dorsal surface and 3% of ventral surface. Major setae on pronotal epipleuron medium in size. Meshes of microsculpture on 30% of disc of pronotum; on 40% of disc of mesonotum; pointed sculpture absent from disc. Mesepisternum without sculpture. Metathorax as mesothorax. Tergum 2 and following entirely covered with microsculpture; pointed sculpture on urogomphus of tergum with narrow scale-like points, absent from anterior band of tergum 9. Sculpture of tergum 10 single-pointed. Pointed sculpture of membrane ventrally on abdomen restricted: extended around hypopleura and behind poststernites.

Third Instar Larvae. Diagnostic combination.- Similar to members of *E. laevigatus* but meshes of microsculpture on 10% of disc of pronotum, and on 40% of disc of mesonotum and metanotum. Distinguished from remaining members by absence of pointed sculpture from mesonotum and metanotum and anterior band of tergum 9.

Third Instar Larvae. Description.- Meshes of microsculpture on 10% of disc of pronotum and 40% of disc of mesonotum and metanotum; pointed sculpture absent from nota, anterior band of tergum 9, and posterior band of terga 1 to 8. Urogomphus of tergum 9 with narrow scale-like sculpture. Abdominal sternite 9 with two accessory setae. Pointed sculpture of membrane extended over most of surface.

Distribution.- The range of this species extends across the southern boreal and cold temperate regions of North America from central British Columbia to Newfoundland south to New Jersey and along the Rocky Mountains to Colorado (Fig. 161). I have examined about 1100 adults and dissected 10 males. I studied five first instar, two second instar, and 10 third instar larvae from George Lake, Alberta.

Collecting notes.- Members live on soft or slightly firm muds exposed to sunlight. In Massachusetts these beetles were common in *Typha* marshes on sun-exposed ground. On the north shore of the St. Lawrence River I found many specimens on firm brown mud among scattered *Carex nigra*. In Gatineau Park, Quebec, I obtained them on the very fine soft muds of an abandoned beaver pond. In Alberta they are commonly obtained from Carex swamps near the Typha zone where Carex rostrata gets more scattered and where thin brown mosses are found above water--an excellent trap for these beetles (adults and larvae) was to cultivate a bit of the Carex zone into a clean black organic mud flat. The larvae live in the same general habitat, usually one to 10 cm above water. This heliophilous species has a life cycle very similar to the one described for members of E. clairvillei. However, I do not know where adults of E. olivaceus overwinter.

Geographical affinities.- Sympatric with E. clairvillei, a member of the cupreus group, and also with E. fuliginosus and E. cicatricosus in eastern North America.

Relationships.- Closely related to E. laevigatus as shown by very dense pleural punctures, the very short apex of the median lobe of males, and lack of apico-internal point on tibia of midleg of males.

3.5.3.14. Elaphrus laevigatus LeConte

Elaphrus laevigatus LeConte 1851: 200. Type locality.- San Francisco, California; type seen by Lindroth (1961) and myself in Museum of Comparative Zoology, Cambridge, Massachussetts. Lindroth 1961: 113.

Elaphrus politus Casey 1897: 345; preoccupied by E. politus LeConte 1851. Type locality.- San Francisco, California; type seen by Lindroth (1961) and myself, in

United States National Museum, Washington, D.C.

Lindroth 1961: 113.

Elaphrus caseyi Leng 1918: 203. New name for the junior homonym proposed by Casey.

Adults. *Diagnostic combination*.- Most similar to members of *E*. *clairvillei* in appearance of dorsal surface but dorsal punctures more scattered and ventral sculpture on pleura very dense (5 to 20 microns apart). Similar to members of *E*. *olivaceus* in many details of punctation on the ventral surface and genitalia but dorsal surface black and very sparsely punctate. Distinct from all members by the presence of two to five punctures in elytral pits and by the very indistinctly outlined setigerous punctures of elytra.

Adults. *Description*.- Upper surface black except for blue-green postero-lateral impressions of pronotum, pits and punctures; ventral surface black with faint golden-green metallic hue; legs and palpi piceous, femur with blue-green metallic hue, and dorsal surface of tibia and tarsomeres with purple metallic hue.

Mentum tooth moderately emarginate; emargination about 0.5 length of tooth. Pronotum with one impression on disc. Intercoxal process of prosternum without accessory setae. Antero-medial surface of metasternum with few punctures, most with setae. Abdominal sternum 7 without or with few indistinct punctures. Abdominal sterna 5 and 6 with about 10 accessory setae, sternum 7 in males with 10 to 20 setae and in females with about five. Pits of elytra with four or five punctures; lateral ridges of pits clearly outlined and clearly fused anteriorly and posteriorly into ring; setigerous punctures very indistinctly outlined. Mirrors indistinctly outlined and not at all contrasted against brilliant intervals 4, 6 and 8. Hind coxae with very few punctures externally and three to five accessory setae near internal margin. Femur of foreleg and midleg with about 40 setae and of hind leg with six setae. Tibia of midleg of males without sharp apico-internal projection between spurs; tibia of foreleg with about 20 setae, and of midleg and hind leg each with about 60 setae.

Integument sculpture. Punctures small (10 to 25 microns in size) on clypeus, head, pronotum, elytral intervals 4, 6 and 8, and coxae; moderate (25 to 30 microns) on pleura and laterally on thoracic band or abdominal sterna. Punctures scattered on pronotum (10 to 200 microns apart), but denser on base of head (about 60 microns apart); punctures dense on pleura (five to 20 microns apart) and moderately dense (25 to 100 microns apart) laterally on thoracic and abdominal sterna. Punctures generally indistinctly outlined on pronotum, elytra and laterally on abdominal sterna; sharply outlined on 33% of circumference of thoracic sterna, and on 50% on pleura.

Alveolae of microsculpture flat in postero-lateral impressions of pronotum and in elytral pits, absent on most of dorsal surface; ventrally alveolae flat.

Male genitalia. Apex of median lobe in dorsal view shortly extended posterior to base of internal sac, very sharp (20 microns wide) and not twisted (Fig. 52a); in lateral view apex moderately widened near internal sac. (Fig. 52b).

Measurements and proportions.- See Table 29.

Variation.- Population samples from localities near San Francisco have smaller means for size measured than samples from Nevada. Though few specimens are available, the means of the following ratios were significantly different EL/EW: 2.73 and EW/HW: 0.805 (i.e. relatively wider elytra). These data are provided as a clue for future studies.

First Instar Larvae. Diagnostic combination.- Similar to members of E. olivaceus but microsculpture generally more expanded: meshes of microsculpture on 50% of dorsal surface and 15% of ventral surface of parietale, alveolae mostly pointed. Meshes of microsculpture on 10% of disc of pronotum, on 50% of disc of mesonotum and metanotum; pointed sculpture near suture on 10% of mesonotum and metanotum, and laterally on 35% of disc of both nota, and on 60% of posterior band of both nota. Distinct from other members by presence of meshes of microsculpture on disc of pronotum.

First Instar Larvae. Description. Seta MP of frontale very small. Setae DMM-A and DMP-A of parietale medium-small; alveolae of microsculpture pointed and on 50% of dorsal surface and 15% of ventral surface of parietale. Setae AII-E

Table 29. Descriptive statistics for E. *laevigatus* based on 10 males and 10 females from San Francisco Co., California.

Character	Range	Mean	1.5SD	2SE	CV (%)
A. Measurements in mm.					
PL	1.6-1.8	1.71	0.098	0.029	3.8
PW	1.8-2.0	1.89	0.116	0.035	4.1
EL	3.9-4.4	4.14	0.240	0.071	3.9
EW	1.3-1.6	1.46	0.115	0.034	5.3
HW	1.7-2.0	1.89	0.113	0.034	4.0
B. Proportions.					
PL/PW	0.868-0.973	0.905	0.040	0.012	2.9
PL/EL	0.400-0.450	0.414	0.017	0.005	2.8
PL/EW	1.110-1.330	1.180	0.074	0.022	4.2
PL/HW	0.875-0.960	0.907	0.032	0.009	2.3
PW/EL	0.439-0.475	0.458	0.012	0.003	1.7
PW/EW	1.250-1.410	1.300	0.058	0.017	3.0
PW/HW	0.973-1.060	1.000	0.034	0.010	2.2
EL/EW	2.750-2.960	2.840	0.090	0.027	2.1
EL/HW	2.120-2.290	2.190	0.073	0.022	2.2
EW/HW	0.720-0.797	0.772	0.032	0.010	2.8

of pronotum large. Meshes of microsculpture on 10% of disc of pronotum, and on 50% of disc of mesonotum; pointed sculpture near suture on 10% of disc and laterally on 35% of disc, and on 60% of posterior band. Metanotum as mesonotum. Setae AII and AIM of terga 1 to 8 medium-small; pointed sculpture of urogomphus of tergum 9 distinctly outlined. Pointed sculpture on abdominal sternite 10, on 30% of surface of ventral membrane of thorax (on prothorax clearly extended toward episternum), and restricted on abdomen to epipleura.

Second Instar Larvae. Diagnostic combination.- Similar to members of E. olivaceus but microsculpture generally more expanded: meshes of microsculpture on 50% of dorsal surface and 10% of ventral surface of parietale; pointed sculpture slightly more contracted on 30% of dorsal and 5% of ventral surface. Meshes of microsculpture on 75% of disc of pronotum, on 90 to 100% of discs of mesonotum and metanotum; pointed sculpture absent from disc of both nota near suture but present laterally on 10% of disc surface. Easily separated from remaining members by absence of pointed sculpture near suture of mesonotum and metanotum, and from anterior band of tergum 9.

Second Instar Larvae. Description.- Meshes of microsculpture on 50% of dorsal surface and 10% of ventral surface of parietale; pointed sculpture less expanded on 30% of dorsal surface and 5% of ventral surface. Major accessory setae of pronotal epipleuron medium-small; meshes of microsculpture on 75% of disc of pronotum, on 90 to 100% of disc of mesonotum and laterally on 10% of disc, but absent near suture. Mesepisternum with fine multi-pointed sculpture. Metathorax as mesothorax. Tergum 2 and following covered with microsculpture; pointed sculpture on urogomphus of tergum 9 narrow scale-like points, absent from anterior band of tergum 9, and sculpture expanded on tergum 10: multi-pointed and scale-like. Pointed sculpture of membrane on ventral surface of abdomen restricted and not expanded around hypopleuron.

Third Instar Larvae. Diagnostic combination.- Similar to members of *E. olivaceus* but microsculpture more expanded, as described under second instar larva and also by presence of pointed sculpture on 5% or more of anterior band of terga 1 to 8. Distinct from remaining members by presence of meshes of microsculpture on pronotum, by lack of pointed sculpture on disc of mesonotum and metanotum, and on anterior band of tergum 9, and by presence of only two accessory setae on abdominal sternite 9.

Third Instar Larvae. Description.- Pointed sculpture absent from lateral surface of disc of mesonotum and metanotum, on 5% or more of anterior band of terga 1 to 8, absent from posterior band of terga 1 to 8. Abdominal sternite 9 with two accessory setae. Pointed sculpture expanded on ventral surface of abdominal membrane.

Derivation of specific epithet.- From latin meaning smooth, probably referring to the smooth appearance of the dorsal surface of adults, resulting from lack of punctures generally.

Distribution.- The range of this species extends from northern California as far south as Los Angeles area and as far east as Reno, Nevada (Fig. 161). I examined 130 adults and dissected 4 males. I studied six first instar, five second instar, and five third instar larvae from San Francisco, California.

United States. CALIFORNIA (4; ANSP, UMRM, DEFW, AMNH): Hullville (2; MCZC); Alameda Co. (3; KSUC, FMNH), Oakland (1; CASC); Fresno Co., Fresno (1; ICCM); Kern Co., Mill Portrero (1; LACM); Lassen Co., Norvell--misspelled Norval (1; CASC), Warmer Valley, Lassen National Forest (1; CASC); Los Angeles Co., Claremont (1; CUIC); Madera Co., Chiquito Creek, 4100' (2; CUIC, USNM), North Fork--misspelled Northfork (3; CUIC, USNM); Marin Co., Inverness (1; CASC), Tamales Bay (1; CASC); Monterey Co., Carmel (3; CASC, UASM), Monterey (2; CASC); Plumas Co., 6 mi. n.w. Chester (1; USNM), 4 mi. w. Quincy (1; UCRC); San Francisco Co., (42; USNM, CASC, MCZC, SEMC), San Francisco (22; USNM, CASC, ANSP, PURC); San Luis Obispo Co., San Luis Obispo (1; FMNH); Sonoma Co., Eldridge (1; CASC); Siskiyou Co., (2; CASC); Trinity Co., Carrville (5; CASC); Tuolumne Co., (1; CASC). NEVADA: Washoe Co., Reno (1; MCZC). NEW YORK: Barre--no doubt mislabelled (1; CUIC).

Collecting notes.- Beetles of this species live on very soft black mud under dead and very dense *Juncus*-like vegetation. General areas are mostly in the shade of deciduous and broad-leaf evergreen trees during the day. This habitat is similar to the one described for *E. clairvillei*. Oviposition took place in the laboratory soon after obtaining adults in April. I saw a slightly teneral adult collected in late September in Warner Valley, Lasse National Forest, Lassen Co. Therefore, in northeastern California populations probably overwinter as adults, and I suspect also along the Pacific coast.

Geographical affinities.- Allopatric but probably sympatric in northeastern California with *E. clairvillei*, a member of the *cupreus* group.

Relationships.- Closely related to *E. olivaceus* as shown by the following shared derived character states: very dense pleural punctures, very short apex of median lobe of males, and lack of apico-internal points on tibia of midleg of males.

3.5.4 Subgenus *Elaphrus* Fabricius

Elaphrus Fabricius 1775: 227. *Type species*.- *Elaphrus riparius* Linnaeus 1775: 407; designated by Latreille 1810: 425. Lindroth 1961: 114.

Trichelaphrus Semenov 1926: 39. Type species.- *Elaphrus riparius* Linneus 1758: 407; Hatch 1951: 113.

Adults. Diagnostic combination.- Eyes with smaller ommatidia on anterior than on posterior surface. Clypeus with four to six setae. Setae of fringe of anterior and posterior margins of pronotum extended to lateral angles (Fig. 20 to 25). Proepimeron and proepisternum apparently fused. Prosternum with setae on disc. Microsculpture of mesosternum formed by large points on intercoxal process, process with setae. Metepisternum without anterior ridge. Basal transverse stria of elytron indistinctly defined at shoulder; surface with one wide mirror near suture (except in E. viridis) (Fig. 115 to 117); pores in punctures very scattered. Tarsomeres 1 to 3 of forelegs of males each with spongy pubescence ventrally; trochanter with three setae; anterior external row of femur with 18 to 21 setae. Trochanter of midleg with three setae. Coxa of hind leg with setae on entire surface. Basal sclerite of ovipositor stylus without spinules apically on ventral surface; apical sclerites with few stout lateral spines.

Adults. Description.- Color of dorsal surface green or copper, in some members upper surface black or copper with dark purple elytra. Dorsal surface densely punctate.

Head. Eyes with smaller ommatidia on anterior surface than on posterior surface. Frons without medial impression (though suggested by elongate punctures and in many members by irregular carinae). Clypeus with four to six setae.

Antennae. Alveolae of microsculpture of antennomeres convex.

Mouthparts. Right mandible grinding edge less than 0.5 of mandible length; basal tooth of retinaculum single, anterior retinacular tooth near terebral tooth (Fig. 4). Stipes with sculpture on ventral surface convex; lacinial teeth subequal. Ligula slightly or not prominent; submentum with eight setae without or with few accessory very small setae; narrow section of gula with convex alveolae of microsculpture.

Thorax. Scimitar-shaped setae of anterior and posterior margins of pronotum very expanded at apex, fringe extended to lateral angles; disc without or with one or two impressions; bead of lateral margin, in most members, interrupted in sinuation and in many specimens without trace of margin left in sinuation. Proepimeron and proepisternum apparently fused. Lateral margin of prosternum slightly sinuate; disc with setae; setae of fringe of anterior margin very expanded apically or in one member narrow.

Process of mesosternum with setae, meshes of microsculpture on intercoxal process formed of large points, and antero-medially formed of fine points.

Metanotum with very small postero-lateral setae. Metepisternum without anterior ridge. Metasternum with setae laterally.

Abdomen. Tergum 7 without setae except on stridulatory scrapers.

Elytra. Striae not defined except for scutellar one; basal transverse stria indistinctly defined at shoulder;

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lateral ridges in pits absent; surface with one large mirror near suture except in some individuals of *E. viridis*; punctures on elytral articulation two to four; pits with 50 to 200 punctures; few punctures with pores on surface (Fig. 20 to 25).

Legs. Trochanter of foreleg with three setae. Femur with 60 to 85 setae; anterior external row with 18 to 21 setae; alveolae of microsculpture convex. Tibia in females with 25 to 40 and in males with 30 to 45 setae; fringe (anterior internal row) 0.67 to 0.75 of length of tibia, fringe without setae posteriorly; posterior medial row in males with 13 to 20 setae and in females with four to six setae. Tarsomeres 1 to 3 of males with spongy pubescence ventrally; tarsomeres 1 to 4 each with six to eight, and tarsomere 5 with two to four spinules underneath.

Alveolae of microsculpture of coxa of hind leg convex. Trochanter with three setae. Femur with 60 to 95 setae; posterior external row with four to 10 setae; alveolae of microsculpture convex. Tibia with 65 to 115 setae. Tarsomeres 1 to 4 each with four to six and tarsomere 5 with two to six spinules.

Coxa of hind leg with setae on surface, surface with one large postero-medial seta and about 30 to 40 medium. Femur with 24 to 31 setae; anterior internal, external and posterior internal rows each with more than three setae; alveolae of microsculpture convex. Tibia with 70 to 95 setae. Tarsomeres 1 to 4 each with six to 10 and tarsomere 5 with two to four spinules ventrally.

Male genitalia. Apex of larger paramere sharp (Fig. 53). Median lobe with apical spatula moderately expanded.

Ovipositor. Basal sclerite of stylus without field of spinules apically on ventral surface; apical sclerite with two to six lateral stout spines, apex without fine setae (Fig. 75).

__First__ __Instar__ __Larvae__. __Diagnostic__ __combination__.- Nasale markedly projected medially; teeth widely separated by large median projection, teeth of nasale absent or extremely small (Fig. 91). Epicranial suture small, less than 0.6 length of antennal scape; angle formed by seta DI-A and pores DI-P and DMP-E less open (90 to 110°), triangle formed by setae DEP, VEP-P and VEM-P very short: anterior angle of triangle open; microsculpture on latero-ventral surface of parietale without scale alveolae. External surface of stipes with unsclerotized band behind postero-lateral seta, external margin entire; setae of dorso-internal 0.5 in apical 0.3 in two rows roughly; postero-ventral pores near each other: internal pore slightly ahead of external one. Seta of lacinia 0.67 or more length of small seta posterior to lacinia. Maxillary palpomere 1 subequal to or smaller than length of palpomere 2. Meshes of microsculpture on surface of disc of pronotum, pointed sculpture on 3 to 5% of disc surface. Size of seta PII-P of mesonotum very small to small; meshes of microsculpture on 60 to 65% of disc surface. Size of seta of epipleuron of mesonotum medium. Metathorax as mesothorax. Size of internal seta of internal poststernite of segments 1 to 9 very small. Pointed sculpture of membrane of abdomen expanded widely along posterior margin of terga 1 to 8.

First Instar Larvae. Description.- Parietale pale laterally or just at base; and terga gray-brown.

Head. Nasale medial projection extremely prominent, teeth widely separated by large medial projection, teeth absent or extremely fine (Fig. 91); pore MPP-E external to egg-burster anterior end, and pore MA-I internal to seta MMA. Epicranial suture less than 0.6 length of antennal scape, head short; convexity of lateral margin in front of neck subequal to one behind neck; size of seta DEP medium, and of seta VMA medium-small; seta DI-A level with postero-lateral angle of frontale, angle formed by seta DI-A and pores DI-P and DMP-E less open (90 to 110|31), system DMM more anterior: seta DMM-P anterior to postero-lateral angle of frontale, triangle formed by setae DEP, VEP-P and VEM-P short: anterior angle open; meshes of microsculpture absent from dorsal and ventral surface (suggested latero-ventrally in some individuals).

Proportions of head (Fig. 77) as follows: PW/PML 1.4 to 1.8, PW/PLP 2.1 to 2.6, PML/PBW 0.8 to 0.9, FW/OL 5.5 to 12.0, PL/OL 4.6 to 8.7, F1/OL 4.0 to 8.3, P1/OL 2.7 to 5.2, and P1/PL 5.0 to 6.2.

Mouthparts. Serration of posterior edge of retinaculum well defined, and on anterior cutting edge absent or defined (Fig. 81). Stipes short: 2.5 to 3.0 times longer than wide; external surface of stipes behind postero-lateral seta with unsclerotized band, margin entire (Fig. 83b). Setae on internal 0.5 of dorsal surface with about 30 setae, setae in apical 0.3 approximating two rows; postero-ventral pores near each other: internal anterior pore slightly ahead of external posterior pore; external 0.5 of stipes dorsal surface with pointed sculpture; seta of lacinia more than 0.6 length of small seta behind lacinia. Seta of galeomere 1 small to medium-small; microsetae along internal side of galeomere 2 in apical 0.3 to 0.1; maxillary palpomere 1 subequal to smaller than palpomere 2. Latero-dorsal spinule of prementum small.

Thorax. Meshes of microsculpture on disc of pronotum, pointed sculpture on 3 to 5% of disc. Seta of proepisternum very small.

Mesonotal seta AIM and AIE-I medium-small to medium, setae PIM-I and PIE-A medium to large, and seta PII-P very small to small; meshes of microsculpture on 60 to 65% of disc surface, pointed sculpture near suture on 30% of disc surface, and pointed sculpture on 15 to 30% of posterior band surface. Mesepimeral seta small. Seta of mesosternite medium-small. Metathorax as mesothorax.

Membrane sculpture on 90% of lateral surface and on 20 to 50% of ventral surface of thorax.

Abdomen. Seta AII and AIM on terga 1 to 8 medium-small, and seta AM-P on tergum 10 very small; pointed sculpture absent from anterior band surface. Anterior epimeral seta of tergum 1 small to medium-small, and tergum 9 very small to small. Seta of sternite on segments 2 to 7 medium-small. Anterior seta of external poststernite of segment 9 small to medium-small. Internal seta of internal poststernite of segments 1 to 9 very small.

Membrane pointed sculpture dorsally expanded widely along posterior margin of terga 1 to 8.

Second Instar Larvae. Diagnostic combination.- Nasale teeth very fine (eroded in some field collected specimens). Dorsal surface near system DMM with zero to five accessory pores. Stipes with external margin projected outward behind postero-lateral seta. Pronotum with about 15 accessory setae and 25 accessory pores; meshes of microsculpture on surface of disc. Mesonotum with eight to 10 accessory setae; pointed sculpture on 30 to 40% of anterior band. Disc of terga 1 to 8 each with seven to nine accessory setae, and disc of tergum 10 without accessory setae, with two accessory pores; pointed sculpture on anterior band of terga 1 to 9. Sternites 2 to 7 with single-pointed sculpture on surface, points scattered. Pointed sculpture of membrane of abdomen expanded dorsally along posterior, lateral and most of anterior margins of terga 1 to 8.

Second Instar Larvae. Description.- Color as first instar larva, in some members base of urogomphus diffusely paler.

Head. Teeth of nasale very small; setae AM-P and MP absent or very small. Parietal seta VMA medium-small; dorsal surface of parietale near system VMM without or with less than six accessory pores; meshes of microsculpture on less than 5% of dorsal surface, meshes absent or barely suggested latero-ventrally.

Mouthparts. Posterior margin of retinaculum and cutting edge smooth. External margin of stipes behind postero-lateral seta projected outward.

Thorax. Disc of pronotum with 15 accessory setae and 25 accessory pores, and pronotal epipleuron with two accessory setae and about five accessory pores. Accessory setae on postero-lateral band of prosternum small. Proepimeron with four accessory pores.

Disc of mesonotum with eight to 10 accessory setae; meshes of microsculpture on 90 to 100% of disc surface, pointed sculpture on 30 to 40% of anterior band surface. Mesepimeral basic seta medium-small; major accessory setae very small to small; sculpture absent. Metanotum as mesonotum.

Abdomen. Basic seta AII and AIM on terga 1 to 8 medium-small, seta MPP-E on tergum 9 very small, seta AM-P of tergum 10 medium-small; surface of terga 1 to 8 each with seven to nine and of tergum 10 without or with accessory setae but with two accessory pores; major basal accessory seta of urogomphus antero-medial in position, seta small to medium; sculpture on terga 1 to 8 single-pointed, pointed sculpture on terga 1 to 9 on all of anterior band surface, and on all of posterior band surface on terga 1 to 8, microsculpture on surface of disc starting on tergum 1, 2 or 4. Hypopleuron of segments 1 to 8 each with four accessory setae; minor accessory setae small to medium-small. Sternites of segments 2 to 8 each with 10 accessory setae, of segment 9 without, and of segment 10 with two major accessory setae; sculpture of segments 2 to 7 single-pointed. External poststernite of segment 1 with three, and of segments 2 to 7 each with two accessory setae. Internal poststernite of segment 1 with one or two, and of segments 2 to 7 each with two accessory setae.

Membrane sculpture expanded dorsally around most of terga 1 to 8 except medio-anteriorly, and over most of ventral side of abdomen.

Third Instar Larvae. Diagnostic combination.- Prementum with about six accessory setae dorso-laterally. Pronotal epipleuron with two accessory setae and about 10 accessory pores. Disc of mesonotum with 23 to 25 accessory setae and 15 to 25 accessory pores, and mesonotal epipleuron with one accessory seta and about six accessory pores; major accessory setae on row behind posterior row of basic setae medium-small to medium; meshes of microsculpture present on entire of disc surface. Epipleuron of segments 2 to 8 each with eight to 14 accessory setae. Hypopleuron of segments 1 to 8 each with eight to 10 accessory setae.

Third Instar Larvae. Description.- Color as in first instar larva; in some members base of urogomphus with well defined paler pattern.

Head. Prementum with six accessory setae dorso-laterally, and with one or two accessory setae antero-laterally; baso-lateral accessory setae medium-small.

Thorax. Disc of pronotum with 21 accessory setae and about 40 accessory pores, and pronotal epipleuron with two accessory setae and about 10 accessory pores; meshes of microsculpture on 80 to 100% of disc surface. Basic proepisternal setae very small to small; surface with about seven accessory setae. Basic proepimeral seta small to very small.

Disc of mesonotum with 23 to 25 accessory setae, and 15 to 25 accessory pores, and mesonotal epipleuron with one accessory seta and about six accessory pores; major accessory setae on row behind posterior row of basic setae medium-small to medium; meshes of microsculpture on all of disc surface. Basic seta of mesepipleuron very small to small; surface with about 15 accessory pores. Mesepimeron without or with two accessory pores. Basic anterior sternite seta small. Metathorax as mesothorax except: anterior pleurite without accessory pores, and major seta extremely small to small.

Abdomen. Knobs of urogomphus on tergum 9 in lateral view medium-large to large, and in dorsal view medium. Basic setae AII and AIM on terga 1 to 8 medium-small to medium, seta PII-P absent to extremely small, seta PI-P on tergum 10 medium-small; disc of terga 1 to 8 each with 17 to 20 accessory setae; pointed sculpture absent or on 40% of anterior band surface. Size of basic anterior seta of epipleuron segments 2 to 5 small to medium-small; disc of segments 2 to 8 each with eight to 14 accessory setae; pointed sculpture on segments 1 and 9. Hypopleuron of segment 1 to 8 each with eight to 10 accessory setae. Sternite of segment 1 with four to eight accessory setae, of segments 2 to 7 each with 12 to 20, of segment 8 with 14 to 20 , of segment 9 without or up to four, and of segment 10 with two major and without or up to two minor accessory setae; accessory setae on segments 2 to 7 small to medium-small. External poststernite of segment 1 with three to seven, and of segments 2 to 7 each with four to nine accessory setae. Internal poststernite of segment 1 with one, and of segments 2 to 7 each with one or two accessory setae.

Distribution.- Members of this subgenus are found across the northern hemisphere from the southern edge of the tundra regions to the southern half of the warm temperate zone (Morocco, southernmost California, northernmost Florida).

3.5.4.1 Key to the species of subgenus *Elaphrus* Fabricius

Adults

1. Pronotum markedly enlarged near middle: lateral margin angulate near middle (Fig. 22 and 23) ...2

1'. Pronotum enlarged or narrower: lateral margin regularly curved (Fig. 20, 21, 24, and 25) 3

2.(1). Dorsal surface brilliant golden-green metallic. Punctures of dorsal surface extremely dense (0 to 5 microns apart) except on copper reflecting surfaces (20 microns apart). Head and pronotum with fine accessory setae on surface. Antennomere 3 with about 20 fine accessory setae and scape with two or three setae. Frons and disc of pronotum without impressions (Fig. 105). Pits of elytron very indistinctly outlined (Fig. 114 and 126). Specimen from California ...*E. viridis* Horn

2'. Dorsal surface dark green metallic. Punctures of dorsal surface less dense: on disc of pronotum 10 microns apart and laterally 40 microns apart. Pronotum with few fine setae. Antennomeres 1 and 3 without accessory setae. Frons with one medial impression and disc of pronotum with two discal impressions (Fig. 105). Pits of elytron very distinctly outlined and very deeply impressed (Fig. 115 and 127). ....*E. lheritieri* Antoine

3.(1'). Pronotum markedly enlarged at middle (Fig. 24); anterior transverse impression partly expressed between medial impression and antero-lateral angles. Antennomere 3 with 30 to 40 setae (Fig. 13), similar to those of following antennomeres; most setae on posterior surface; antennomere 2 without accessory setae. Specimen from natural prairie land of North America .E. lecontei Crotch

3'. Pronotum less enlarged at middle (Fig. 20, 21, and 25); anterior transverse impression not expressed. Antennomere 3 without accessory setae or with less than 30 accessory setae--then antennomere 2 with one or two accessory setae (Fig. 11 and 12); setae generally distributed around antennomere. 4

4.(3'). Punctures of pronotum very large (40 to 50 microns in size), but on elytral pits much smaller (25 microns). Lateral margin of pronotum beaded along most of its length including sinuation (Fig. 20). Punctures of pronotum quite uniformly dense: on disc about 20 microns apart and laterally about 30 microns apart. Specimen from mountains of western North America ....E. new species A

4'. Punctures of pronotum less than 35 microns in size. Punctures of elytral pits subequal to or slightly smaller than those of pronotum. Lateral margin of pronotum not beaded or barely so in sinuation (Fig. 21 and 25). Punctures of pronotum twice as dense on disc of pronotum as laterally, or uniformly dense--then punctures only 5 microns apart. 5

5.(4'). Pronotum and head with numerous fine accessory setae on surface. Antennomere 3 without accessory setae. Punctures of pronotum as dense on disc as laterally (about 5 microns apart). Pronotum with lateral margin more rounded (Fig. 21). Specimen from California ....*E*. new species B

5'. Pronotum and head without accessory fine setae, or with few setae submedially-- then antennomere 3 with 10 to 20 accessory setae. Punctures of pronotum twice as dense on disc as laterally. ..6

6.(5'). Side of pleuron black with faint metallic hue; pleuron markedly contrasted against green or copper metallic abdomen. Punctures of pleura especially on proepisternum seemingly larger (about 60 microns in diameter) as surface around punctures depressed--thus puncture only 30 to 40 microns (Fig. 109). Pronotum with two discal impressions in most specimens. Specimen from eastern North America. ....*E*. *ruscarius* Say

6'. Side of pleuron metallic and of similar color to abdomen. Punctures of pleura especially proepisternum seemingly smaller (30 to 40 microns) as surface around puncture little or not depressed. Pronotum without or with one or two impressions on disc. 7

7.(6'). Subapex of hind femur in dorsal view with three to seven long (150 microns in length) white setae (Fig. 35). 8

7'. Subapex of hind femur in dorsal view without or with one to three short (40 microns in length) white setae (Fig. 34). 9

8.(7). Accessory setae of abdominal sterna 4, 5 and 6 mostly between ambulatory setae, not extended laterally on punctate area (Fig. 140). Punctures of pronotum and elytral pits smaller (25 microns). In most specimens disc of pronotum with two impressions. Punctures of proepisternum very dense (0 to 10 microns apart) and partly sharply outlined on 50% of circumference along posterior rim. Lateral punctures of abdominal sternum 4 numerous (about 150). Specimen from North America . ...*E. californicus* Mannerheim

8'. Accessory setae on abdominal sterna 4, 5 or 6 extended laterally in punctate area (Fig. 141). Punctures of pronotum and elytral pits larger (30 microns in size). Pronotum with one indistinctly outlined discal impression, or impression absent. Punctures of proepisternum about 25 microns apart and sharply outlined on most of puncture circumference. Lateral punctures of abdominal sternum 4 less numerous (40 to 80). Specimen from northeastern China or Japan. ....*E.* species C

9. (7'). Accessory setae on abdominal sterna 4, 5 or 6 extended laterally toward lateral margin in punctate area (in very few individuals not extended) (Fig. 141). Pronotum without or with one indistinct impression on disc. 12

9'. Accessory setae of abdominal sterna 4, 5 and 6 not extended laterally into punctate area (Fig. 140) toward lateral margin (in very few specimens extended laterally--then pronotal punctures smaller (25 microns) and pronotum of most specimens with two discal impressions). 10

10. (9'). Punctures of pronotum 25 to 30 microns in size. Punctures on pleura especially on proepisternum less dense (about 30 microns apart), and sharply outlined on most of circumference, Antennomere 3 without accessory setae. Setae of parameres of males shorter than width of narrowest paramere (Fig. 62b). Specimen from the Chinese province of Sinkiang and adjacent USSR. .E. hypocrita Semenov

10'. Punctures of pronotum of most specimens 20 to 25 microns. Punctures of pleura especially on proepisternum denser (0 to 20 microns apart--average 15 microns) and sharply outlined on 50 to 70% of circumference. Antennomere 3 without or in Canadian specimens with 10 to 20 accessory setae. Setae of parameres of males longer than width of narrowest paramere (Fig. 67c). Specimen from

North America. 11

11.(10'). Median lobe of males relatively longer. Apex of median lobe in lateral view wide (Fig. 66b). in ventral view narrow (10 microns) and twisted (Fig. 66a). Specimen from California, central Oregon east of Cascades, or from localities in southern Idaho, Utah, Colorado or Arizona. ....E. finitimus Casey complex

11'. Median lobe of male relatively shorter: Apex of median lobe in lateral view narrow except for specimens from northern Great Basin (Fig. 67b to 69b); in dorsal view apex wide (35 microns) not twisted except for specimens from northern Great Basin (Fig. 67a to 69a). Specimen from regions north and east of states named above but sympatric along the Rocky Mountains of Montana, Wyoming, and Colorado. ....E. americanus Dejean complex

12.(9). Alveolae of microsculpture very convex especially on abdominal sterna. Abdominal microsculpture of very sharp and elevated scale-like alveolae. Antennomere 3 without accessory setae. Elytra of most specimens with one row of distinct mirrors. ....E. riparius Linnaeus

12'. Alveolae of microsculpture flat or in some specimens subconvex on abdominal sterna; pointed sculpture restricted to base of abdomen near hind coxae and alveolae not elevated (Fig. 144). Pronotum of some specimens with fine accessory setae on disc. Antennomere 3 with about 20 accessory setae and antennomere 2 of most specimens with one or two accessory setae. Specimen with one, two or three rows of distinctly outlined mirrors. 13

13. (12'). Punctures of abdominal sternum 4 less numerous (0 to 40 -- usually 20) (Fig. 142). Pronotum of many or most specimens with fine accessory setae on disc. Punctures in pits scattered, thus punctures separated by two to four rows of meshes of microsculpture (Fig. 136). Punctures of proepisternum sharply defined on most of circumference. 14

13'. Punctures of abdominal sternum 4 numerous (40 to 70) (Fig. 141). Pronotum of very few specimens with fine accessory setae on disc. Punctures in pit less scattered, thus punctures separated by one or three rows of meshes of microsculpture. Punctures of proepisternum outlined sharply over 70% of circumference. Specimen from subarctic Eurasia or western North America. ....E. tuberculatus Mäklin complex

14. (13). Punctures of elytral pit smaller (20 microns), but larger on pronotum (25 microns). Specimen from eastern Tibetan region, China.

..............................*E. tibetanus* Semenov

14'. Punctures of dorsal surface 25 to 30 microns in size. Specimen from northwestern North America or Commander Islands, USSR. ...*E. parviceps* Van Dyke

First instar larvae

1. Cutting edge of mandible not toothed. Epicranial suture very short: 0.2 to 0.25 length of antennal scape. Anterior seta of abdominal epipleura 1 to 8 very small. Specimen from North America.
.......................*E. californicus* Mannerheim

1'. Cutting edge of mandible toothed. Epicranial suture longer: 0.3 to 0.6 length of antennal scape. Anterior seta of at least abdominal epipleura 4 and 5 small or larger, and very small on segment 9 at least. 2

2.(1'). Seta AIM similar in size on terga 1 to 8 or slightly smaller posteriorly. 3

2'. Seta AIM abruptly much smaller on any of terga 5 to 8. 5

3.(2). Seta MP of frontale virtually absent. Occipital suture rather short: 0.3 length of antennal scape. Seta VMP-A of parietale medium-small, and seta MI of pronotum small. Specimen from Eurasia.
..............................*E. riparius* Linnaeus

3'. Seta MP of frontale very small. Occipital suture longer: 0.4 to 0.5 length of antennal scape. Seta

VMP-A of parietale medium, and seta MI of pronotum medium-small. Specimen from North America 4

4.(3'). Nasale with very fine teeth. Pointed sculpture of membrane ventrally on prothorax not extended to proepisternum. Dorsum of parietale mostly dark except near eye and along base. Seta VEM-P and DMM-A of parietale medium-small. Specimen from northwestern North America.
...................E. tuberculatus Mäklin complex

4'. Nasale without teeth. Pointed sculpture of membrane ventrally on prothorax extended to proepisternum. External 0.5 of dorsum of parietale pale. Setae VEM-P and DMM-A of parietale very small. ....E. lecontei Crotch

5.(2'). Nasale distinctly toothed. Anterior seta of abdominal epipleuron 4 small.
...........................E. americanus Dejean

5'. Nasale not toothed. Anterior seta of abdominal epipleuron 4 medium-small. ......E. ruscarius Say

Second instar larvae

1. Pointed sculpture near suture of mesonotum and metanotum extended on 30% of disc. 2

1'. Pointed sculpture near suture absent from disc of mesonotum and on 3% of disc of metanotum. 3

2.(1). Major accessory setae of pronotal epipleuron very small. Seta AM-P of tergum 10 medium-small. Occipital suture very short: 0.2 to 0.25 length of antennal scape. ....E. californicus Mannerheim

2'. Major accessory setae of pronotal epipleuron medium-small. Seta AM-P of tergum 10 medium. Occipital suture much longer: 0.5 to 0.6 length of antennal scape. ....E. americanus Dejean

3. (1'). Major accessory setae on row behind posterior row of basic setae small. Pointed sculpture on dorsal surface of stipes expanded along length. Pointed sculpture of membrane fine. ...E. lecontei Crotch

3'. Major accessory setae on row behind posterior row of basic setae medium-small. Pointed sculpture on dorsal surface of stipes restricted to basal 0.5. Pointed sculpture of membrane very strongly expressed or very fine. 4

4. (3'). Pointed sculpture of membrane very strongly expressed. Major accessory setae of pronotal epipleuron medium-small. Major accessory seta at base of urogomphus medium. Specimen from northwestern North America.

...................E. tuberculatus Mäklin complex

4'. Pointed sculpture of membrane very fine. Major setae of pronotal epipleuron very small. Major accessory setae at base of urogomphus medium-small or smaller. Specimen from Eurasia.

.........................E. riparius Linnaeus

Third instar larva

1. Pointed sculpture absent from disc of metanotum or barely suggested. 2

1'. Pointed sculpture on 5% or more of disc near suture of metanotum. 5

2.(1). Terga 1 to 3 partly covered with pointed sculpture. ....*E. ruscarius* Say

2'. Pointed sculpture on disc of terga 1 or 2 and following. 3

3.(2'). Abdominal sternite 10 with two minor accessory setae and two major accessory setae on each side. Pointed sculpture laterally on 10 to 15% of disc of mesonotum and metanotum. ....*E. californicus* Mannerheim

3'. Abdominal sternite 10 without minor accessory setae but with two major accessory setae on each side. Pointed sculpture absent laterally from disc of mesonotum and metanotum. 4

4.(3'). Pointed sculpture on abdominal epipleura 2 to 4 and membrane very fine. Urogomphus dark brown, but anterior surface of tergum 9 pale. Major accessory setae on pronotal, mesonotal and metanotal epipleura very small. Specimen from Eurasia. ....*E. riparius* Linnaeus

4'. Pointed sculpture on abdominal epipleura 2 to 4 clearly expressed, and very markedly expressed on membrane. Urogomphus pale, but anterior surface of tergum 9 dark brown. Major accessory setae of pronotal, mesonotal and metanotal epipleura medium-small. Specimen from northwestern North America. ....E. tuberculatus Mäklin complex

5. (1'). Seta AM-P of tergum 10 small. Pointed sculpture absent from anterior band surface, and 30% of posterior band of terga 1 to 8.
..............................E. finitimus Casey

5'. Seta AM-P of tergum 10 medium-small. Pointed sculpture on 40% of anterior band surface, and on 80% or more of posterior band surface of terga 1 to 8. 6

6. (5'). Major accessory seta on metathoracic anterior pleurite small. Seta AIM similar in size on terga 1 to 8. Seta MI of pronotum small. Pointed sculpture on 15% of anterior band of mesonotum and metanotum. ....E. lecontei Crotch

6'. Major accessory seta on metathoracic anterior pleurite virtually absent. Seta AIM abruptly much smaller on any terga from 5 to 8. Seta MI of pronotum medium-small. Pointed sculpture on 40% of anterior band of mesonotum and metanotum.
............................E. americanus Dejean

3.5.4.2 List of Species of Subgenus *Elaphrus* Fabricius

E. new species A. *Type area*.- mountains of Colorado.

E. new species B. *Type locality*.- Anguin, California.

E. ruscarius Say 1834: 417. *Type locality*.- Pennsylvania--designated by Lindroth 1961: 119. Lindroth 1961: 119.

E. texanus Casey 1924: 17. *Type locality*.- Galveston, Texas; type (seen by Lindroth and me) in United States Museum of Natural History, Washington, D.C. Lindroth 1961: 119.

E. lecontei Crotch 1873: 246. *Type locality*.- Longs Peak, Colorado; type (seen by Lindroth and me) in Museum of Comparative Zoology, Cambridge, Massachussetts. Lindroth 1961: 114.

E. devinctus Casey 1920: 139. *Type locality*.- Wray, Colorado; type (seen by Lindroth and me) in United States National Museum of Natural History, Washington, D.C. Lindroth 1961: 114.

E. spissocornis Casey 1924: 18. *Type locality*.- Parowan, Utah; type (seen by Lindroth and me) in United States National Museum of Natural History, Washington, D.C. Lindroth 1961: 114.

E. lheritieri Antoine 1947: 26. *Type locality*.- near Sofi, Morocco. Antoine 1955: 47. I have seen topotypes.

E. californicus Mannerheim 1843: 190. *Type locality*.- California. Lectotype designated by Lindroth in

Zoological Museum, University, Helsinki, Finland. Lindroth 1961: 118.

_E_. _similis_ Leconte 1848: 449. _Type_ _locality_.- Longs Peak, Colorado; type (seen by Lindroth and me) in Museum cf Comparative Zoology, Cambridge Massachussetts. Lindroth 1961: 118.

_E_. _hesperius_ Casey 1920: 138. _Type_ _locality_.- Humbolt Co., California; type (seen by Lindroth and me) in United States National Museum of Natural History, Washington, D.C. Lindroth 1961: 118.

_E_. species C. Known from northeastern China and Japan.

_E_. _hypocrita_ Semenov 1926: 39. _Type_ _area_.- Russian Turkestan. I have seen Banninger labelled specimens.

_E_. _viridis_ Horn 1878: 52. _Type_ _locality_.- California. Lindroth 1961: 110.

_E_. _horni_ Csiki (1927: 420). New name for _E_. _viridis_ Horn, a junior homonym of _E_. _viridis_ Letzner 1849: 52. Lindroth (1961: 110) rejected Csiki's name as Letzner's name refers to a color variation of _E_. _riparius_ and therefore does not fall under the rules of priority.

_E_. _finitimus_ Casey 1920: 137. _Type_ _locality_.- California; type (seen by me) in United States National Museum of Natural History, Washington, D.C.

_E_. _ruscarius_ _foveatus_ Pierce 1948a: 54. _Type_ _locality_.- McKittrick (Asphalt field, site 4, depth 4 feet);

type (seen by me) in the Los Angeles County Museum of Natural History, Los Angeles, California. NEW SYNONYM.

E. americanus Dejean 1831: 558. Type locality.- Great Bear Lake, N.W.T.; designated by Lindroth 1961: 115. type (seen by Lindroth 1961: 115) in Museum of National d'Histoire Naturelle, Paris, France.Lindroth 1961: 115.

E. intermedius Kirby 1837: 62. Type locality.- Great Bear Lake, N.W.T.; type (seen by Lindroth 1961: 115) in British Museum of Natural History. Lindroth 1961: 115.

E. punctatissimus LeConte 1850: 210. Type locality.- Sault Ste. Marie, Mich.; type (seen by Lindroth and me) in Museum of Comparative Zoology; Cambridge Massachussetts. Lindroth 1961: 115.

E. sinuatus LeConte 1850: 210. Type locality.- Pic, Ontario on the north shore of Lake Superior; type (seen by Lindroth and me) in Museum of Comparative Zoology; Cambridge Mass. Lindroth 1961: 115.

E. gratiosus Mannerheim 1853: 118. Type locality.- Kaktnu River, Kenai Peninsula, Alaska; type (seen by Lindroth) in Zoological Museum, University, Helsinki, Finland. Lindroth 1961: 115.

E. bituberosus Casey 1924: 17. Type locality.- Terrace, British Columbia; type (seen by Lindroth and me) in United States National Museum, Washington, D.C.

Lindroth 1961: 115.

E. tuberculatus Mäkl 1877: 16. Type area.- Arctic Russia. Semenov 1904: 20, and 1910: 433.

  E. latipennis Sahlberg 1880: 10. Type area.- Arctic Russia. Semenov 1910: 433.

  E. latipennis costulifera Semenov 1904: 125. Type area.- Arctic Russia. Semenov 1904: 20.

  E. tuberculatus normalis Poppius 1908: 4. Semenov 1910: 433.

  E. latipennis orientalis Semenov 1904: 20. Type locality.- lower Lena River.

  E. tuberculatus orientalis Semenov. Semenov's new combination. Semenov 1910: 433.

E. riparius Linnaeus 1758: 407. Type locality.- Uppsala, Sweden-- designated by Lindroth 1961: 116. Type (seen by Lindroth 1957: 339) in the Linnaean Collection, London, England. Lindroth 1961: 116.

  E. viridis Letzner 1849: 52. Lindroth 1961: 110.

  E. riparius ab. nigrescens Letzner 1849: 52.

E. parviceps Van Dyke 1925: 112. Type locality.- Seward Peninsula, Alaska; Type (seen by Lindroth and me) in the California Academy of Sciences, San Francisco, California. Lindroth 1961: 116.

E. tibetanus Semenov 1904: 22. Type area.- eastern Tibet.

Incertae sedis

E. *smaragdiceps* Semenov 1889: 354. *Type* *locality*.- China, Kansu, Dshoni (8820') in the mountains of Amdo region.

E. *paludosus* Olivier 1790: 5.

E. *baschkiricus* Motschulsky 1844: 72. *Type* *locality*.- Baschkiria.

E. *dilaticollis* Sahlberg 1844: 22. *Type* *locality*.- Ockotsk (spelled Ochotsk), USSR.

E. *violaceomacultus* Motschulsky 1845: 337. *Type* *locality*.- Kamtsckatka, USSR.

E. *latiusculus* Motschulsky 1850: 5. *Type* *locality*.- Dauria.

E. *altratulus* Wagner 1917: 259.

E. *riparius* *ab* *rubescens* Antoine 1920: 9.

E. *riparius* *ab*. *cupritarsis* Bänninger 1919: 148.

3.5.5 Subgenus *Elaphroterus* Semenov

Elaphroterus Semenov, 1895: 308. *Type* *species*.- *Elaphrus* *aureus* Müller, 1821, designated by Semenov, 1926. Lindroth 1961: 119.

Elaphrotatus Semenov, 1895: 308. *Type* *species*.- *Elaphrus* *punctatus* Motschulsky, 1844: 73. Designated by Semenov 1895: 308.

Adults. *Diagnostic* *combination*.- Maxillary palpomere 3

0.3 length of palpomere 4. Submentum with six large and few small setae. Fringe of setae along anterior and posterior margins of pronotum extended to lateral angles. Prosternal disc without setae; intercoxal process of prosternum glabrous or setose. Mesosternal process without setae. Sterna 5 and 6 with 10 to 15 setae. Trochanter of foreleg with two setae. Trochanter of midleg with one or two setae. Setae on inner 0.5 of hind coxa. Apical sclerite of stylus of ovipositor without lateral stout spines and apical setae.

Adults. Description.- Dorsal color grayish green to brilliant green, in some individuals head copper, remaining green or most of body reddish copper with grayish disc of elytra, or elytra blackish with gray disc. Upper surface quite densely to very densely punctate.

Head. Eyes with thin cornea, ommatidia slightly smaller on anterior than on posterior surface. Alveolae of microsculpture convex on labrum.

Antennae. Alveolae of microsculpture convex on antennomeres.

Mouthparts. Right mandible cutting edge less than 0.5 length of mandible; basal retinacular tooth single and apical retinacular tooth near terebral tooth. Maxillary palpomere 3 0.3 length of palpomere 4. Galeomere 1 1.5 length of maxillary palpomere 2. Alveolae of microsculpture on ventral surface of stipes convex. Teeth on lacinia subequal in length. Submentum with six large setae and few small ones; alveolae of microsculpture in narrowest part of gula convex.

Thorax. Setae of fringe along anterior and posterior margins of pronotum extended to lateral angles, setae moderately expanded apically; lateral margin complete to absent; disc without or with one discal impression. Prosternum without setae or with few setae on prosternal process, setae of fringe moderately expanded apically.

Mesosternal process without setae; pointed sculpture on process and antero-medially.

Metanotal postero-lateral setae very small. Metepisternal anterior ridge absent or poorly defined; lateral surface without or with lateral setae.

Abdomen. Tergum 7 without setae except on stridulatory scraper plates. Sterna 5 and 6 each with 10 to 15 setae.

Elytra. Striae absent or scutellar one suggested; lateral ridges absent from pits; interval 3 with one to three major mirrors (Fig. 116); pits with 25 or more punctures; punctures with pores common though less than in members of subgenus Elaphrus, discal setigerous punctures large (40 to 50 microns), punctures at elytral articulation indistinctly delimited and few (two to four).

Legs. Trochanter of foreleg with two setae; meshes of microsculpture flat. Femur with 45 to 55 setae, anterior internal row with about 13 setae and internal row with two to three setae; meshes of microsculpture flat. Tibia in females with 17 to 20 and in males with 25 to 27 setae, fringe (antero-internal row) 0.67 length of tibia and without setae behind, postero-medial row in males with nine to 13 and in females with two setae. Tarsomeres 1 to 3 of males without or with spongy pubescence ventrally; tarsomeres 1 to 4 each with six and tarsomere 5 with four spinules.

Alveolae of microsculpture on coxa of midleg convex or flat. Trochanter with one or two setae. Femur with 35 to 50 setae, anterior internal row with five to seven and internal row without or with as many as four setae; meshes of microsculpture convex or flat. Tibia with about 70 setae. Tarsomeres 1 to 4 each with four to 10, and tarsomere 5 with four to six spinules.

Setae of coxae of hind leg with setae on internal 0.5: one large and three to 20 of medium size, 10 to 60% of punctures with setae. Femur with 18 to 21 setae, antero-internal row with eight setae, internal row without setae, posterior external row with three to five setae; alveolae of microsculpture convex or flat. Tibia with 65 to 80 setae. Tarsomeres 1 to 4 each with 10 to 12 and tarsomere 5 with four to six spinules.

Male genitalia. Largest paramere with sharp apex (Fig. 53b), spatula of median lobe apex moderately wide or wider, internal sac without basal large scales.

Ovipositor. Apico-ventral surface of basal sclerite without spinules, apical sclerite without spines or setae, apical setae absent (Fig. 74).

First Instar Larvae. Diagnostic combination.- Nasale with medial point extremely projected, teeth separated by moderately large medial points, teeth small but larger than in members of subgenus Elaphrus (Fig. 92). Seta EA-E on frontale small. Epicranial suture 0.6 or less length of antennal scape, lateral convexity in front of neck subequal to one behind neck; pointed sculpture on ventro-lateral side of parietale present on 2 to 25% of surface. Apical 0.3 of internal brush on dorsal surface of stipes roughly in two to five rows; postero-ventral pores near each other: internal one slightly anterior to external one; maxillary palpomere 1 subequal to or smaller than palpomere 2. Disc of pronotum with meshes of microsculpture on 60% of surface. Pointed sculpture on 50 or 100% of posterior band surface of mesonotum and metanotum. Pointed sculpture on all of anterior band of terga 1 to 8. Pointed sculpture on 90% of ventral surface of membrane and expanded widely behind terga 1 to 8.

First Instar Larvae. Description.- Pale laterally on dorsal surface, and pale over most of ventral surface of head. Nota piceous and terga grayish brown.

Head. Medial point of nasale extremely projected, teeth separated by moderately large medial point, teeth small though larger than in members of subgenus Elaphrus (Fig. 92); size of seta EA-E small; pore MMP-E external to anterior end of egg-bursters, pore MA-I internal to seta MMA. Epicranial suture 0.6 or less length of antennal scape;

lateral convexity in front of neck subequal to one behind neck; size of seta DMP-A medium and of seta VMA medium-small; system DMM anterior to baso-lateral angle of frontale, angle formed by seta DI-A and pores DI-P and DMP-E less open (about 90 to 110°), triangle formed by setae DEP, VEM-P and VEP-P very short: anterior angle very open; pointed sculpture on 2 to 25% of ventral surface.

Head proportions (Fig. 77) as follows: PW/PLP 1.9 to 2.5, PML/PBW 0.8 to 1.1, FW/OL 6.0 to 12.0, PL/OL 5.6 to 9.6, F1/OL 4.4 to 9.2, P1/OL 2.6 to 5.2, and P1/PL 4.6 to 5.9.

Mouthparts. Posterior edge of retinaculum and apical cutting edge of mandible toothed or not. Stipes short: 2.5 times longer than wide, margin behind externo-lateral seta projected outward, anterior face of projection unsclerotized; brush of setae in internal 0.5 of dorsal surface very dense (40 to 50 setae), setae in apical 0.3 approximately two to five rows; postero-ventral pores near each other: internal one slightly ahead of external one. Maxillary palpomere 1 subequal to or smaller than palpomere 2. Seta on galeomere 1 small to medium-small, microseta on internal side of galeomere 2 in apical 0.4 to 0.1. Apical seta of lacinia 0.8 to 1.0 length of seta on stipes posterior to lacinia. Antero-dorsal spinule of prementum medium-small.

Thorax. Disc of pronotum with meshes of microsculpture on 60% of surface, pointed sculpture absent. Mesonotal setae

AIM and AIE-I small to medium-small, setae PIM-I and PIE-A medium small to medium-large, seta PII-P small; meshes of microsculpture on 60 to 65% of disc surface, pointed sculpture on 50 or 100% of posterior band surface. Size of mesosternite seta medium. Metathorax as mesothorax.

Pointed sculpture on 85 to 90% of ventral and lateral surface of membrane.

Abdomen. Pointed sculpture on all of anterior band surface of terga 1 to 8, sculpture on urogomphus of tergum 9 single pointed and extended over entire surface. Size of anterior epipleural seta of segment 1 small to medium. Sternite seta of segments 2 to 7 medium-small; pointed sculpture absent from segments 1 to 7, present on 15% of segment 8 and on 30% of segment 9. Anterior seta of external poststernite of segments 1 to 8 small to medium-small and on segment 9 medium-small.

Pointed sculpture of membrane widely expanded behind terga 1 to 8, and very expanded on most of lateral and ventral surfaces.

Second Instar Larvae. _Diagnostic combination_.- Disc of pronotum with 25 to 45 accessory setae, and pronotal epipleuron with three accessory setae and no accessory pores. Disc of mesonotum with 20 to 40 accessory setae. Pointed sculpture laterally on 25 to 35% of mesonotal anterior band surface. Major basal accessory seta of urogomphus dorso-medial in position; sculpture of terga 1 to

8 multi-pointed on disc, pointed sculpture present on all of anterior and posterior band surfaces. Membrane sculpture on abdomen extending partly in front of terga 1 to 8 and expanded ventrally around sternites.

Second Instar Larvae. Description.- Color similar to first instar larva except in members of E. ulrichi (described under this species).

Head. Size of basic seta EA-E of frontale small to medium-small. Parietale with five to seven accessory pores near system DMM.

Mouthparts. Posterior edge of retinaculum and apical cutting edge smooth. External margin of stipes behind postero-lateral seta very protruded, anterior face of extrusion unsclerotized, dorso-lateral basic spinule of prementum small; dorso-lateral surface with six to 15 and latero-anterior margin with one to three accessory setae.

Thorax. Disc of pronotum with 25 to 45 accessory setae, and pronotal epipleuron with three accessory setae and no accessory pores; meshes of microsculpture on 10 to 20% of surface. Accessory setae of proepisternum small; surface with six or seven accessory setae. Basic proepimeral seta very small to medium-small.

Disc of mesonotum with 20 to 40 accessory setae; meshes of microsculpture on all of disc surface, pointed sculpture laterally on 25 to 30% of disc surface, and on all of anterior band surface. Basic mesepimeral seta medium-small. Metathorax as mesothorax.

Abdomen. Basic setae PI-P and AM-P on tergum 10 medium-small to medium, and of seta MPP-E on tergum 9 small; disc of terga 1 to 8 with 16 to 28 accessory setae; basal major accessory seta of urogomphus dorso-medial in position; sculpture on terga 1 to 8 multi-pointed, pointed sculpture present over all of anterior band surface on terga 1 to 9 and on all of posterior band on terga 1 to 8, sculpture on tergum surface starting on tergum 1. Minor accessory setae on hypopleuron of segments 1 to 8 small or slightly larger. Sternite of segment 8 with 12 to 14, of segment 9 with six or less accessory setae, and on segment 10 with six minor accessory setae; sculpture single-pointed, points scattered.

Membrane sculpture dorsally and ventrally on most of surface.

Third Instar Larvae. Diagnostic combination.- Mesonotal epipleuron with one to five accessory setae and two or less accessory pores. Mesepipleuron with two to four major accessory setae and about 15 accessory pores. Major medial knob of urogomphus in lateral view small to extremely small. Disc of terga 1 to 8 each with 40 to 55 accessory setae; meshes of microsculpture present on entire disc surface. Sternite of segments 2 to 7 each with 30 to 40 accessory setae.

Third Instar Larvae. Description.- Color as first instar, base of urogomphus in some members paler.

Mouthparts. Prementum with 10 to 15 dorso-lateral accessory setae.

Thorax. Size of major accessory setae on row behind posterior row of basic setae small to medium-small. Size of accessory proepisternal setae very small to medium; surface with 10 accessory setae.

Disc of mesonotum with 30 to 55 accessory setae, mesonotal epipleuron with one to five accessory setae and two or less accessory pores; size of major accessory setae on row behind posterior row of basic setae small to medium-small. Mesepipleuron with two to 12 accessory setae and about 15 accessory pores; size of major accessory setae small. Mesepimeron with two or less accessory pores; size of basic seta small. Metathorax as mesothorax except anterior pleurite with one accessory seta, and seta very small to small.

Abdomen. Major medial knob of urogomphus in lateral view small to extremely small. and in dorsal view medium to virtually absent; discs of terga 1 to 8 each with 40 to 55 accessory setae, epipleuron of terga 1 to 8 each with eight to 25 accessory setae; meshes of microsculpture on entire surface. Epipleuron of segments 2 to 8 each with 17 to 40 accessory setae; pointed sculpture developed. Hypopleuron of segments 1 to 8 each with 12 to 22 accessory setae. Sternite of segment 1 with 14 to 18 accessory setae, of segments 2 to 7 each with 25 to 40, of segment 8 with 25 to 40, of segment 9 with four to 12, and of segment 10 with five to 12 accessory setae; sculpture on segments 2 to 7 multi-pointed, weakly or well defined. Internal poststernite with two to five accessory setae.

Membrane sculpture expanded ventrally.

Distribution.- Members of this subgenus are found across Eurasia to western North America from subarctic regions to the northern half of the warm temperate zones (central France; Caucasus; Honshu Island, Japan; central California).

3.5.5.1 Key to the Species and Subspecies of Subgenus *Elaphroterus* Semenov

Adults

1. Dorsal surface with very faint brassy hue. Alveolae of microsculpture absent or flat over most of dorsal and ventral surfaces in elytral pits flat or convex (Fig. 124). Punctures very large especially on pronotum (45 microns in size). Trochanter of midleg with two setae. Tarsomeres of foreleg of males not expanded and without spongy pubescence ventrally. Specimen from eastern Asia. ......*E. punctatus* Motschulsky

1'. Dorsal surface metallic green, gray-green or copper. Alveolae of microsculpture convex on dorsal surface or partly absent from or flat on copper surface of pronotum and intervals 4, 6 and

8 (Fig. 125); alveolae flat or convex ventrally. Punctures smaller (30 microns in size) on pronotum. Trochanter of midleg with one seta. Tarsomeres 1 to 3 of males slightly enlarged and with spongy pubescence ventrally. 2

2.(1'). Pronotal lateral margin in vertical plane beaded, bead extended along most of margin except in sinuation. Intercoxal process of prosternum of many specimens with one or two accessory setae. Specimen from cold temperate regions of Europe, isolated in Caucasus Mountains. .E. aureus Müller

2'. Pronotal lateral margin in vertical plane rounded, angular or barely beaded near middle; bead absent or barely expressed at middle. Intercoxal process of prosternum without accessory setae. 3

3.(2'). Pronotum with lateral margin in vertical plane rounded or barely angulate near middle (Fig. 27). Femur testaceous except two green metallic spots, one medially and one apically. Tibia of foreleg of male with very large sharp projection at base of posterior spur-- best seen in posterior view of tibia (Fig. 149). Specimen from western North America. ....E. purpurans Hausen

3'. Pronotal lateral margin in vertical plane angular, in lateral view this line extended on much of margin length (Fig. 26). Femur red-brown or piceus, dorsal surface green metallic not divided in two spots. Tibia of foreleg of male without projection at base of posterior spur. Specimen from Eurasia or northwestern North America. 4

4. (3'). Pronotum with many bright copper reflecting surfaces. Dorsal surface brighter as alveolae of microsculpture flat on or absent from elytral intervals 4, 6 and 8, pronotum and head. Postero-lateral angle without proximal setigerous puncture. Dorsal surface of head, pronotum and side of elytron brilliant golden-green metallic. Elytron with one or two rows of indistinctly outlined mirrors. Accessory setae absent from posterior surface of metasternum. Specimen from middle Europe. ....*E. ulrichi* Redtenbacher

4'. Pronotum without strongly reflecting copper surface. Dorsal surface dull, alveolae of microsculpture convex except on mirrors. Postero-lateral angle of pronotum with proximal setigerous punctures. Dorsal surface duller green, gray-green or copper. Elytron with three rows of distinctly outlined mirrors (Fig. 116). Accessory setae on posterior surface of metasternum. Specimen from boreal and subarctic Eurasia or northwestern North America. 5

5. (4'). Dorsal surface of elytron smoother, pits little

impressed and mirrors flat. Punctures on most specimens in intervals 4, 6 and 8 less dense (30 to 40 microns apart). Pronotum without accessory setae on disc. Coxa of hind leg with two to five accessory setae on disc. Lateral surface of metasternum without accessory setae. Abdominal sterna 4, 5 and 6 with one to eight accessory setae. Color gray-green. Specimen from locality in western Europe or eastward to Yenessey River. ....E. angusticollis jakowlewi Semenov

5'. Dorsal surface of elytron coarser, pits more deeply impressed and mirrors convex (Fig. 116). Punctures of most specimens denser (10 to 20 microns apart) on intervals 4, 6 and 8 (Fig. 125). Pronotum of 50% of specimens with accessory setae on disc. Coxa of hind leg with setae more abundant on inner 0.5 (10 to 20 setae). Lateral surface of metasternum with many accessory setae. Abdominal sterna 4, 5 and 6 with 10 to 20 accessory setae. Color green with green legs, or gray-green with copper femur and clypeus, or red-copper except sutural and apical area of elytra. Specimen from locality in northwestern North America, or as far west as Lena River in Siberia. ....E. angusticollis angusticollis Sahlberg

First Instar Larvae

1. Internal cutting edge of mandible above retinaculum very distinctly toothed. Pointed sculpture latero-ventrally on 2% of parietale, and on 50% of posterior band of mesonotum and metanotum. Specimen from middle Europe and Caucasus Mountains. ....E. aureus Müller

1'. Internal cutting edge of mandible above retinaculum indistinctly toothed or not toothed. Pointed sculpture latero-ventrally on 10% or more of surface of parietale, and on 100% of posterior band of mesonotum and metanotum. 2

2.(1'). Meshes of microsculpture laterally on 20% of dorsal surface of parietale; pointed sculpture absent from parietale dorsal surface. Setae AII-E, MI and ME-I of disc of pronotum medium in size. Specimen from western North America. ....E. purpurans Hausen

2'. Meshes of microsculpture laterally on 40% or more of parietale dorsal surface; pointed sculpture laterally on 20% or more of parietale dorsal surface. Setae AII-E, MI and ME-I of disc of pronotum small. 3

3.(2'). Posterior edge of retinaculum and cutting edge anterior to retinaculum toothed. Pointed sculpture extended laterally on 40% of dorsal surface of parietale, and near suture on 30% of disc of mesonotum and metanotum. Specimen from northwestern North America west to Lena River, USSR. ....*E. angusticollis angusticollis* Sahlberg

3'. Posterior edge of retinaculum and cutting edge of mandible anterior to retinaculum not toothed. Pointed sculpture on 20% of parietale dorsal surface, and near suture of mesonotum and metanotum absent from disc. Specimen from middle Europe. ....*E. ulrichi* Redtenbacher

Second Instar Larvae

1. Meshes of microsculpture absent from latero-ventral surface of parietale. Abdominal tergum 10 without accessory setae. Disc of mesonotum and metanotum with about 20 accessory setae on each side. Specimen from middle Europe. ....*E. aureus* Müller

1'. Meshes of microsculpture laterally on 5% or more of parietale ventral surface. Tergum 10 with one pair of accessory setae. Disc of mesonotum and metanotum with about 40 accessory setae on each side. 2

2.(1'). Meshes of microsculpture restricted baso-laterally to 5% of parietale ventral surface. Pointed sculpture near suture of mesonotum and metanotum on 1 to 3% of disc. Disc of terga 1 to 7 each with about 16 accessory setae on each side. ....E. purpurans Hausen

2'. Meshes of microsculpture baso-laterally on 10% of parietale ventral surface. Pointed sculpture near suture of mesonotum and metanotum on 30% of disc. Disc of terga 1 to 7 with about 30 accessory setae on each side. 3

3.(2'). Setae EMP and MP of frontale small to very small. Pointed sculpture of membrane very markedly expressed. Dorsum of parietale near frontale, nota and terga 1 to 9 dark brown and urogomphus of tergum 9 red-brown. Specimen from locality in northwestern North America west to Lena River, USSR. ....E. angusticollis angusticollis Sahlberg

3'. Setae EMP and MP of frontale virtually absent. Pointed sculpture of membrane very fine. Surface posterior to eyes on dorsum of parietale, pronotum, tergum 1, and lateral 0.33 of terga 2 to 7 testaceous; mesonotum and metanotum, internal 0.67 of terga 2 to 7, and terga 8 and 9 dark brown; urogomphus of tergum 9 red-brown. Specimen from middle Europe.
.........................E. ulrichi Redtenbacher

Third Instar Larvae

1. Meshes of microsculpture absent from latero-

ventral surface of parietale. Tergum 10 without accessory setae. Disc of pronotum covered with meshes of microsculpture. Specimen from middle Europe and Caucasus Mountains. ..*E. aureus* Müller

1'. Meshes of microsculpture laterally on 5% of ventral surface of parietale. Tergum 10 with one pair of accessory setae. Meshes of microsculpture on 75% of disc of pronotum. 2

2.(1'). Pointed sculpture laterally on 2% of dorsal surface of parietale. Meshes of microsculpture near neck on 5% of parietale ventral surface. Posterior band of mesonotum and metanotum without accessory setae. Specimen from western North America. ....*E. purpurans* Hausen

2'. Pointed sculpture laterally on 20% of dorsal surface of parietale. Meshes of microsculpture laterally on 15% of parietale ventral surface. Posterior band of mesonotum and metanotum with one or two accessory setae laterally. 3

3.(2'). Setae EMP and MP of frontale small to very small. Tergal epipleura 1 to 8 typically narrow, each with about 10 to 15 accessory setae. Dorsum of parietale pale except for brown area near frontale; nota and terga 1 to 9 dark brown. Membrane sculpture very strongly expressed. Specimen from locality in northwestern North America west to Lena River, USSR.

..........E. angusticollis angusticollis Sahlberg

3'. - Setae EMP and MP of frontale virtually absent. Tergal epipleuron very much expanded with about 25 accessory setae. Surface behind eyes, base of parietale, pronotum, tergum 1, external 0.33 of terga 2 to 7 testaceous; mesonotum, metanotum, internal 0.67 of terga 2 to 7, and terga 8 and 9 dark brown. Specimen from middle Europe.

........................E. ulrichi Redtenbacher

3.5.5.3 List of Species of Subgenus Elaphroterus Semenov

E. punctatus Motschulsky 1844: 73. Type locality.- Lake Baikal, USSR.

  E. cribatus Semenov 1889: 353. Type locality.- China, Kansu, Amdo.

E. aureus Müller 1821: 229. Type area.- Middle Europe.

  E. littoralis Dejean 1826: 275. Type area.- Hungary.

  E. smaragdinus Reitter 1887: 241. Type locality.- Czechoslovakia.

  E. tschitscherini Semenov 1897: 595. Type area.- Caucasus. Semenov 1926: 40.

E. purpurans Hausen 1891: 251. Type locality.- British Columbia; type deposition unknown. Lindroth 1961: 119.

  E. pallipes Horn 1878: 51. Type locality.- Oregon; type (seen by Lindroth 1961: 119) in Academy of Natural Sciences, Philadelphia, Pennsylvania. It is a junior homonym of Asaphidion pallipes Duftschmid described originally as an Elaphrus (Silfverberg pers. comm.).

E. angusticollis angusticollis Sahlberg 1844: 20. Type locality.- Okhotsk USSR (spelled Ochotsk). I have seen 1 topotype. Palmén 1944: 17-25.

E. angusticollis jakowlevi Semenov 1895: 303. New status. Type locality.- Jamburg near Leningrad, USSR. I have seen topotypes. Palmén 1944: 17-25.

Incertae sedis

E. angustatus Chaudoir 1850: 161.

E. longicollis Sahlberg 1880: 11.

E. jakowlevi ab costulatus Semenov 1895: 385.

E. ulrichi Redtenbacher 1842: 5. Type area.- Middle Europe.

E. beraneki Reitter 1887: 242.

4.0 Classification

4.1 Introduction

A systematic work, in addition to defining taxa and providing keys for identification of specimens, should provide a classification based on an evolutionary hypothesis. Such an hypothesis is important because this is the means of relating unique patterns of taxa to evolutionary theory, the central core of biology. Systematics indeed makes its ultimate explanation with the evolutionary theory. It provides an hypothesis about evolutionary relationships between taxa. Based primarily on structural features of adults, it predicts other systems of reference: biochemical, behavioral, chromosomal, and larval. It infers important evidence about past zoogeographical events. Finally, it shows, if desired, the degree of divergence between taxa (Ashlock, 1975).

Schools of thought.- There are two major schools of thought for classification of living things: the phenetic (represented by some pheneticists) and evolutionary-cladistic schools.

These pheneticists, or numerical taxonomists, achieve their classification in two steps. First, they determine the degree of similarity of taxa under study. Similarity is estimated by various statistical methods. All characters are either equally or unequally weighted. The results are expressed as a percent of similarity or as a spatial distribution of clusters (Sokal and Sneath, 1963). Second, classification is erected by assembling similar taxa into groups with or without help of phenon lines (i.e. 75% phenon line may represent the subgenus level and intersecting lines may be named).

Members of the evolutionary-cladistic school also achieve their classification in two steps. First, they attempt to reconstruct the probable phyletic relationships of taxa studied. This is done by associating taxa that share a derived state of one or more characters (synapomorphic state (Hennig, 1966)). Second a classification is built. This step is achieved in two ways. First, cladists classify by recency of common descent where any taxon of category above species includes all descendants of the common ancestor of this taxon, without considering differentiation among taxa. Therefore, any taxa of a category above species level is holophytic (Ashlock, 1975). Also, cladists determine the category level by the time of presumed appearance of the common ancestor. Second, "evolutionists" in their classification erect higher taxa that are derived from a single ancestor but may or may not include all descendants of this common ancestor. Therefore, if a small monophyletic group among a larger monophyletic group is judged unusually well-differentiated, it may be elevated as a taxon of the level of the inclusive larger group. Thus "evolutionists" accept paraphyletic taxa. Both subdivisions of the evolutionary-cladistic school reject polyphyletic higher taxa, while pheneticists (those using phenograms for classification) do not consider these concepts of holophyly, monophyly, paraphyly, and polyphyly.

Rohlf (1963) and Steward (1968) both analyzed adults and larvae of Aedes by phenetic methods based on numerous characters. Results of species association are generally congruent, but associations at higher levels are generally incongruent. Both works are extremely enlightening, as they illustrate that adults and larvae not only are very different looking animals living under very different conditions, but they are probably evolving under these different conditions relatively independently and at their own rate. While studying adults and larvae of Elaphrini, I came quite easily to the same conclusion.

If the classification is truly evolutionary, then one expects congruent results no matter what system of reference is used or stage studied because sister groups are decendants of a single ancestor. Since the evolutionary rates were rather different between adults and larvae of Elaphrini, I had ideal material to test techniques for congruency and to sort out, hopefully, the one most likely to provide a consistent evolutionary hypothesis. I was especially interested, after a preliminary study, in determining relationships of three very distinct taxa (Diacheila, Blethisa, Elaphrus), generally ranked as genera, represented by adults and larvae. With so few units, there are only three possible ways to pair these genera. I have included in this analysis the subgenera of Elaphrus. Another important reason for working at this level was that I had excellent representation of adults and larvae for these higher taxa and the quality of data was excellent for both numerical and cladistic analysis.

Objectives.- In the following discussion, I establish relationships of the genera and subgenera of Elaphrini using separately the procedures of the phenetic and evolutionary-cladistic methods. The purpose is to compare results between both systems and to test each system for congruency of results based on adults and larvae. Therefore four systems of relationships will be presented: two phenetic systems for adults and larvae, and two evolutionary-cladistic systems (hereafter referred to as phylogenetic) for adults and larvae.

4.1.1 Phenetic Association

Numerical methods.- In this analysis, I used any characters with states distributed quite uniformly within genera and subgenera and excluded characteristics of species level. For each character, I coded the states between zero and one. These values for the states of this character are attributed to each taxon. Then the value of the state for each taxon was compared to each taxon. If the state for two taxa was similar, I recorded zero; if the state value was different, I subtracted one from the other and retained the result as an absolute value. If a character is expressed in a higher taxon as two or more states, the numerical values of these states are added and divided by the number of states in this taxon. This was done for all characters. Finally, the absolute difference of all characters for all possible pairs was determined. The result was divided by the number of characters and expressed as a percent of similarity. The results were then expressed as a phenogram. The index of dissimilarity is expressed as follows:

Index of dissimilarity in percent = $(\mathrm{sum}(|X_i - X_j|) \times 100)/N$

X = character state value for taxa "i" and "j"

N = number of characters used

The index of similarity is the index of dissimilarity subtracted from 100.

Results of numerical classification of adults and larvae.- Tables 30 and 31 show the coded values and distribution for each character state. Phenograms for adults and larvae are illustrated in Fig. 168.

At the generic level, adults of *Blethisa* and *Diacheila* are more similar to one another (64%) than both are to adults of *Elaphrus* (35%). The adults of four subgenera of *Elaphrus* are associated in two groups of two subgenera each. Adults of *Arctelaphrus* are more similar to those of

Neoelaphrus (85%) than to any other. Adults of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (85%). Adults of both groups of subgenera are similar in 70% of character states.

At the genus level, larvae of *Diacheila* and *Elaphrus* are more similar (57% of character states of first instar larvae, 59% of second instar larvae) than both are to larvae of *Blethisa* (39% of character states of first instar larvae, 27% of second instar larvae). Larvae of the four subgenera of *Elaphrus* are associated in two groups of two subgenera each. Larvae of *Arctelaphrus* are more similar to larvae of *Neoelaphrus* (86% of character states of first instar larvae, 84% of second instar larvae) than to any other. Larvae of subgenus *Elaphrus* are more similar to those of *Elaphroterus* (76% of character states of first instar larvae, 86% of second instar larvae).

4.1.2 Phylogenetic Reconstruction

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Cladistic methods.- Whitehead (1972) described in detail the logic for use of biological species concept and other general aspects of biology related to phylogenetics. I accept his view. Here, briefly, is the working method used in the study of phylogeny of Elaphrini.

Evolutionary relationships of taxa are determined by recognition of sister taxa. Two or more taxa are likely to share a common ancestor if they share a derived state of a character (Hennig's (1966) synapomorphic character states). The grouping is termed monophyletic, as all taxa included are descendents of one common ancestor. This process is repeated until all sister taxa have been recognized.

The main problem is to recognize a derived state (Hennig's (1966) apomorphic state) from an ancestral one (Hennig's (1966) plesiomorphic state). This task is difficult since for only a few character states is it easy (i.e. the elytral structures of Elaphrus adults are quite clearly derived). Ross (1974) and Ball (1975) summarize the basic approaches. Conditions of character states are determined by: ex-group comparisons, in-group comparisons, and group trends. A special form of multi-state character is the morphocline.

Ex-group comparisons.- If the state of a character, expressed in some members of the taxon studied, exists among taxa of at least the next higher category, it is likely a less derived state. This is based on the assumption that their extensive distribution is the result of inheritance, not of independent evolution. However, as pointed out by Ekis (1977), a state, originally widespread among taxa, following massive extinction may be sparsely distributed among surviving taxa, and, relict states should be carefully considered when using this type of evidence. Therefore, the state is likely to be ancestral. For example, the lateral margin of the pronotum of members of many carabid tribes related to Elaphrini show two setae: one near the middle and one near the postero-lateral angle. Therefore the presence of these setae in members of Diacheila and Blethisa is probably ancestral while the absence of the middle one from members of Elaphrus is considered derived.

Characters with three or more states are segregated into one ancestral and two or more derived states. For some characters, these derived states appear to be derived independently (i.e. the dorsal colour in members of Neoelaphrus, green, is considered ancestral; while, dark copper, brown copper, and silvery, are considered derived and probably independently so). For other multi-state characters, if the states appear to be derived from one another, (therfore forming a logical suite of derived states) they are arranged into a morphocline.

As an example of a morphocline, striae 2 and 3 in Diacheila are straight and no catenations are formed. This is considered the ancestral state when compared with other elaphrines. In members of B. eschscholtzi these two striae are in contact before and after the setigerous punctures--the setigerous puncture is in the middle of a circle made by the striae. This state is derived as it is not seen in other carabids. In other members of Blethisa the striae are in contact only before the setigerous puncture. This is a derived state rarely expressed in other carabids. However, B. eschscholtzi is least derived, as suggested by the evolution of the apex of the male median lobe; thus the catenation in other members of *Blethisa* is considered derived and evolved from the *B. eschscholtzi* type. In members of *Elaphrus* the striae arrangement is similar to *B. eschscholtzi* but the striae are very indistinct or absent and the circle of striae or punctures is large (it is termed pit). Thus, the *Elaphrus* pit is evolved from *B. eschscholtzi* type. Therefore, we have two morphoclines: *Diacheila*-*B. eschscholtzi*-*Elaphrus* and *B. eschscholtzi*-other *Blethisa*.

Group trends.- In many independent lineages, some characters, under some circumstances, are likely to be expressed similarly. For example, adult cave beetles that are only distantly related, in the sense that they were derived from different ancestors, resemble one another closely in the following respects: body pale, appendages very long, hind wings absent, metepisterna shortened, humeri eliminated, eyes lost, tactile setae elongated. In members of *Elaphrus*, a trend is expressed relative to dorsal puncture density in relation to habitat. Punctures are much denser if adults of various species occur on surfaces free from vegetation and coarse organic debris. For species of sun exposed habitats, the size and density of punctures on the dorsal surface are correlated with soil particles, therefore finer and denser punctures are associated with beetles that normally run on soil of fine particles.

I assumed that ancestors of *Elaphrus* were adapted to sun exposed surfaces, but adults of species associated with shady habitats have scattered punctures on the dorsal surface. Therefore, scattered punctures on the dorsal surface is a derived state that occurred independently a few times. Among adults of species associated with sunny surfaces those occurring on clay of stream banks or on very fine clays of alkaline ponds, punctures are finer and denser. These two habitats are considered as more recently occupied habitats among _Elaphrus_. Therefore, finer and denser punctures are probably derived, and evolved independently a few times.

In-group comparisons.- For some characters, states cannot be interpreted in ex-group comparisons because the information is lacking (a common situation with elaphrine larvae) or the expression of the state in other groups is not known. Determination of the ancestral condition of the state is suggested by finding which state is the least derived complex.

For example, in adults the fringe along the posterior margin of the pronotum is terminated before the postero-lateral impression, behind the impression, or at the hind angle. Ex-group evidence based on broscines and melaenines suggests that the fringe terminated at the hind angle is derived. I could not decide about the other two states. In-group evidence suggests that the fringe terminated behind the postero-lateral impressions is ancestral as it is in members of _Diacheila_. Therefore, this state (in members of

Arctelaphrus and members of the *uliginosus* group in *Neoelaphrus*) is ancestral and gave rise to the state where the fringe is ended before the impression (other *Neoelaphrus* groups) and to the state where the fringe extends to hind angles (members of *Elaphrus* and *Elaphroterus*).

Results of phylogenetic reconstruction.- Data presented in tables 32 to 37 are used in the reconstruction of the phylogenetic diagrams (Fig. 169). In these tables, each character is coded by one letter or a combination of two letters. The derived state is represented by the capital symbols. Where three or more states are presented, if the two or more derived states arose independently, an integer (or for a lost state (-)) is added to the letter code. If the states are part of a morphocline, I use ('), ("), etc. after the letter code, suggesting the cline progression. The basis of judgement is expressed as "1" for ex group evidence and as "2" for in-group evidence, and "3" group-trend evidence.

Results.- At the genus level, results of analysis of relationships among adults show that *Elaphrus* shares a common ancestor with *Blethisa*, and that both of these genera share a common ancestor with *Diacheila*. At the subgenus level *Elaphrus* and *Elaphroterus* share a common ancestor, *Neoelaphrus* shares a common ancestor with the above subgenera, and *Arctelaphrus* shares a common ancestor with the above three subgenera.

At the genus and subgenus level, results of relationships among larvae show similar results to those described above for adults. However, I failed to show the relationships of *Neoelaphrus* relative fo *Arctelaphrus*.

4.2 Comparisons Between Systems of Association

The three genera among the cladograms and the phenograms were paired three ways: one system based on phenetic relationships of adults, one based on phenetic relationships of larvae, and one based on phylogenetic relationships of adults and larvae. Therefore, phenograms based on adults and larvae are incongruent while the cladograms based on adults and larvae are congruent.

The subgenera of *Elaphrus* are associated similarly on phenograms based on adults and larvae and in cladograms based on adults and larvae. However, the relationships of *Neoelaphrus* are dissimilar between phenograms and cladograms. On phenograms *Neoelaphrus* is associated with *Arctelaphrus*; while on cladograms, based on adults, *Neoelaphrus* is the sister-group of the *Elaphrus*-*Elaphroterus* group, and *Arctelaphrus* is the sister group of all three subgenera.

The phylogenetic reconstruction based independently on adults and larvae is congruent. However, the cladogram based on larvae was difficult to construct since evidence of character state distribution is very limited (most previous descriptions of larvae are superficial and hence do not provide data needed for analysis of relationships).

Three genera can be paired only three ways. The numerical analysis produces two systems: Blethisa and Diacheila most similar for adults, and Diacheila and Elaphrus most similar for larvae. The phylogenetic results based on adults suggests that Blethisa and Elaphrus are more closely related. Similar results were obtained with larvae, but I feel the evidence is not as solid. Obviously, one of these classifications is right.

4.3 Conclusions

Numerical analysis.- The incongruent results between adults and larvae in the numerical analysis can be explained by various factors: insufficient data, incorrect numerical technique, or even incorrect coding of states, or that phenetic principles do not apply for phylogenetic reconstruction.

In statistical work, one expects to approach the real mean as sample size increases. How many characters are necessary to reach consistent results? In my first analysis of adults (based on one Diacheila, two Blethisa, and 13 Elaphrus species), I used 288 characters. The results obtained were consistent at the generic level with classifications based on 88 characters from pleura and sterna of thorax, and abdominal sterna; on 57 characters from the head and tergites, cn 51 characters from dorsum of the head, the pronotum and the elytra; and on 87 characters from legs. The only discrepancy was at the subgeneric level of genus Elaphrus where Arctelaphrus is marginally associated with subgenus Elaphrus for the leg characters. Therefore, in using 80 to 120 characteristics in analysis of adults and larvae, I probably had enough characters.

I used the simplest index of similarity. Obviously, more complex cluster analysis techniques exist. However, the taxa compared are very distinct. Therefore, I do not suspect many differences due to techniques for the association of these genera.

Coding can be criticized since in about 40% of characteristics used, more than two states are expressed. However, I obtained very similar results using only two-state characters in subanalysis of adults and larvae.

As I used probably enough characters in these analyses, and satisfactory methods, I feel that the incongruent results between genera based on adults and larvae suggest that some basic philosophical principles are fundamentally wrong in the formulation of taxa association.

Pheneticists measure gaps (percent of similarity) between taxa (OTU's of Sokal and Sneath, 1963). Gaps are caused by two factors: extinction of intermediate taxa and evolutionary rates. The extinction effect, though important in the classification process, is not important in working out relationships. However, evolutionary rates are probably the most important factor to explain the incongruent results.

Assume that species at any stage are evolving at similar rates. Then the overall changes should be less among recently evolved taxa than between older ones. Therefore, phenograms based on different stages not only would be congruent, but the phenogram would be a phylogenetic reconstruction. However, evolutionary rates not only are different between species at any stage, but these rates are not correlated with other stages.

Therefore, since evolutionary rates are not uniform, phenograms based on different stages are likely to be incongruent. Phenograms reflect a mixture of effects due to evolutionary rates and recency of descent. Fast evolving taxa are likely to be singled out as Elaphrus at adult stage, or Blethisa at larval stage, or slow evolving taxa are likely to be associated such as Diacheila and Blethisa at adult stage, and Diacheila and Elaphrus at larval stage. Therefore, the principle of assembling living things based on overall similarity of equally weighted characters is not likely to formulate consistently a phylogenetic hypothesis. I feel such techniques have their place in groups of animals or plants with very immature classification. This method measures distinctness and should not be used for purposes of phylogenetic reconstruction.

Cladistic analysis.- The phylogenetic reconstructions based separately on adults and larvae are congruent despite the different evolutionary rates between species at any stage and uncorrelated evolutionary rates between stages. I feel some of the evidence shown to unite Blethisa to Elaphrus based on adults and larvae is based on high weight character states. Because of this I feel that the cladistic reconstruction is the one that is most likely to provide an evolutionary hypothesis. As far as any elaphrine reconstruction is concerned only further work will clarify the problem.

4.4 Classification of Elaphrini

Classification involves establishment of formal ranks, and location of taxa under study within a system of higher taxa. In the phylogenetic system of Hennig (1966), taxa are monophyletic and holophyletic (Ashlock, 1975), and are ranked according to inferred age of origin. In the so-called "evolutionary" system, taxa are monophyletic (holophyletic), or paraphyletic, and are ranked according to criteria of divergence, diversity and relative age (Simpson, 1961; Mayr, 1969).

Supra-specific ranks used in this study are four: tribe, genus, subgenus, and species group. This number seems sufficient to encompass the limited diversity and to portray the major features of evolution of the species. The data presented establish that each higher taxon is clearly delimited by autapomorphic character states, and that each of the three groups currently ranked as a genus is clearly distinguished from all others. At a higher level, this applies to the tribe Elaphrini, as currently accepted, and at a lower level, to the subgenera of *Elaphrus*. Thus, in recognizing taxa, I have adhered first to the principle of monophyly of the cladistic system, and second to the canons of divergence and diversity of the "evolutionary" system.

I have not felt it necessary or desirable to recognize a formal taxon to include *Blethisa* and *Elaphrus* apart from *Diacheila* because of the limited diversity of the Elaphrini, nor to group the subgenera of *Elaphrus*.

My contribution to classification of this group has been two-fold: first, to arrange the taxa in a phylogenetic sequence, and second, to seek the sister group of the Elaphrini, in order to locate the tribe in the general system of the Carabidae.

Inter-group relationships: the search for the elaphrine sister groups.- Jeannel (1941, 1942) discussed relationships of the elaphrines to other carabid tribes . He put them near the southern hemisphere Megadopini. Among his "Caraboidea Simplicia", members of Megadopini and Elaphrini share similar setose parameres. However, setose parameres are probably an ancestral state shared with various taxa generally recognized as primitive carabids, and with Broscini, Patrobini, Nomiini, Melaenini, and Scaritini, among more evolved tribes. However, *Elaphrus* adults have a narrow metepimeron which should locate the tribe near Jeannel's "Caraboidea Limbata, Scrobifera or Stylifera". Bell (1967) put the Elaphrini in the Isopleuri with Loricerini, Scaritini, and Cicindelini. I remained puzzled for many years feeling that Megadopini are not related to Elaphrini, and that Broscini seem close to them. During this period, I failed to demonstrate the existence of shared derived characteristics between any of the tribes with setose parameres. The first clue was from Ball's (1956) study of broscine male genitalia. I felt that I could homologize the complex posterior sclerites x and y seen in his Broscina with the elaphrine stylet and anterior cup-shaped sclerite. Sclerite x of these Broscina is made of two long dorsal adjacent sclerites, and is membranous ventrally; the ejaculatory duct penetrates the posterior end. My observation remained at this level until Ball brought to my attention the male genitalia of a little known tribe, the Melaenini, where the sclerite x is similar to those of Diacheila specimens. As in Broscina, the Melaenus adults studied have conjunct middle coxal cavities and the metepimeron is absent or narrow and fused.

I feel that, since sclerites x and y are probably derived states, the Elaphrini, Melaenini and the subtribe Broscina, should be considered related. Because I have only this evidence, I cannot say if in the remaining Broscini and other tribes with setose parameres this state was lost or did not evolve. Moreover, I cannot say if a long stylet-like sclerite x is derived relative to the shorter sclerite of males of Broscina. I failed to find other shared and derived character states between elaphrines and melaenines or between elaphrines and broscines.

In the study of character state distribution outside the elaphrines, I refer to the Broscina and the Melaenini, but I referred to many other tribes of carabids for a more comprehensive overview.

In the general frame of carabid classification, the Elaphrini and its related groups, the Melaenini and the Broscina, are related to the Nomiini, the Patrobini, and the remaining subtribes of the Broscini. They share with most members of these tribes setose parameres (an ancestral character state) and a posterior transverse impression behind the eyes (probably a shared derived character state). The relation of these subtribes and tribes to elaphrines is not clear.

Relationships among genera and subgenera of Elaphrini based on adults.- The relationships among the three extant genera remained uncertain for a few years of my study. Lindroth (1954) and I were puzzled by the complex distribution of characteristics among the three elaphrine genera which make it difficult to determine inter-group relationships. The best clue came in his description of _B. eschscholtzi_ with pupillate setigerous punctures. I did not appreciate this until I saw a female of this species (Fig.

29) Striae 2 and 3, and 4 and 5, are in contact before the setigerous puncture, surround it until in contact behind it, then are parallel until the next puncture. This complex organization of striae is seen in members of *Elaphrus* subgenera *Arctelaphrus* and *Neoelaphrus*. Moreover, *B. eschscholtzi* is the least derived *Blethisa* as suggested by the apex of the median lobe and the pronotum. Later I found more features supporting the close relationship between *Elaphrus* and *Blethisa*: their ancestor developed an enlarged posterior end of stylet of the median lobe for muscle attachment linking the stylet to the very thickly sclerotized base of the median lobe. With this and other evidence, I believe it very unlikely that these states would be regressed in *Diacheila* without a trace, and believe that this genus is the plesiomorphic sister group of the *Blethisa*-*Elaphrus* lineage.

The naturalness of each genus was easily demonstrated and was congruently supported by numerical data (see detail in Fig. 169a): the ancestor of *Diacheila* evolved narrow and scimitar-shaped setae on prosternal anterior margin; those of *Blethisa*, evolved octagonal frontal grooves; and those of *Elaphrus*, evolved elytral pits and mirrors, and prominent eyes.

The species of *Elaphrus* were grouped by Semenov (1926) into five subgenera of which four are retained here. These groups were not recognized by Jeannel (1942) but were recognized by Lindroth (1961).

The monophyly of each subgenus is clearly suggested by autapoypic character states indicated in Fig. 169a.

Associating subgenera was easy except in deciding relationships between _Arctelaphrus_ and _Neoelaphrus_. The main axis of subgeneric orientation is the morphocline of reduction of apical setae on apical sclerites of the stylus of the ovipositor. _Arctelaphrus_ females have two very small setae, the ancestor of _Neoelaphrus_ lost one, and those of _Elaphroterus_ and _Elaphrus_ lost both. This theme is supported by the setigerous punctures of the elytra, which are small (30 microns) in members of _Arctelaphrus_ and have enlarged (40 - 60 microns) in the common ancestor of the remaining subgenera. Moreover, accessory setae on the intercoxal process of the prosternum in the least derived members of _Neoelaphrus_ and _Elaphroterus_ suggests that the accessory setae on the disc is a more ancestral trait. _Neoelaphrus_ is less derived than _Elaphrus_ and _Elaphroterus_. These last-named subgenera are clearly sister groups as their common ancestor evolved the unusual corneal specialization (thin and thick zones) of the eye, and lost both apical setae from the apical sclerite of the ovipositor stylus.

Relationships among species of subgenus Neoelaphrus based on adults.- The species of _Neoelaphrus_ are arranged in three groups. The naturalness of each group is suggested by the following shared derived character states (see Fig. 170 for details). The ancestor of the _uliginosus_ group gained four to six impressions on each side of the pronotal disc, and the pronotal lateral margin in lateral view became sinuate near middle; those of the fuliginosus group gained a cuticular projection at the base of the anterior spur and posterior spur of male foretibia, and evolved very thick (100 microns) cornea of eye; and those of the cupreus group evolved a narrower (10 to 15 microns) bead on lateral margin of pronotum.

The main axis in orienting these three groups was the area of termination of the fringe of the pronotal posterior margin. In members of Diacheila and Arctelaphrus the fringe is terminated behind the postero-lateral impression (40 to 120 microns from hind angle). Therefore I consider as derived a fringe ended before the postero-lateral impression (200 to 250 microns from hind angle). Thus, the fuliginosus group and the cupreus group are sister groups.

The uliginosus group has four and probably five known species. E. uliginosus and E. pyrenaeus are sister species as suggested by the thick and twisted apex of the male median lobe in dorsal view. E. splendidus is least derived. Because of lack of morphological and chorological evidence, I do not know if E. japonicus is ancestral to E. splendidus, or shares a common recent ancestor with E. uliginosus and E. pyrenaeus

The fuliginosus group has three extant species. E. fuliginosus was easily recognized as least derived: the complete and wide bead of the pronotal lateral margin. E.

lindrothi and *E. cicatricosus* are sister species, as their common ancestor lost the bead on lateral margin of pronotum, and the accessory setae on abdominal sterna 5, 6 and 7 of both sexes.

The *cupreus* group has five extant species. Those species are arranged in two subgroups: the ancestor of the *sibiricus* subgroup evolved very elongate and wide (in lateral view) apex of the male median lobe; and those of the *clairvillei* subgroup gained a brilliant dorsal surface (lack of sculpture or meshes under smooth transparent layer), and their lateral ridges of elytral pits became fused. In the *sibiricus* subgroup two species are known: *E. cupreus* and *E. sibiricus*. This latter species is more conservative because of dorsal color and puncture density. The *clairvillei* subgroup has three species. *E. olivaceus* and *E. laevigatus* are considered sister species as their common ancestor evolved very dense pleural punctation, very short median lobe apex, finer dorsal punctures and lost the apico-internal projection on male midtibia. I consider *E. clairvillei* least derived of the three.

Relationships among genera and subgenera of Elaphrini based on larvae.- Evidence in reconstructing the elaphrine phylogeny is limited. The reason is not lack of characters, but rather lack of ex-group evidence and difficulty in homologizing setal character states. Briefly, synapomorphic evidence confirms many adult groupings, other associations seem less solidly backed, while in one the evidence is lacking.

Larvae of *D. arctica* are least derived as suggested by presence of a conical lacinia, a widespread state in carabids. Larvae of *D. polita* are very similar to those of *D. arctica*, but the lacinial seta is extremely small, as in members of *Blethisa*.

The close relationship of *Blethisa* and *Elaphrus* is suggested by the following shared derived states: increased number of accessory setae on all sclerites of the second and third instar larvae, and by larger seta on galeomere 1. In these two characteristics, larvae of *Diacheila* are more similar to members of other tribes. The naturalness of each genus was demonstrated by autapotypic character states indicated in Fig. 169b.

The common ancestor of *Elaphrus* and *Elaphroterus* evolved a shorter head, shorter epicranial suture, and the presence of two or more rows of setae in apical 0.33 dorso-internal surface of stipes. *Arctelaphrus* appears less derived than *Neoelaphrus* as its members show an unsclerotized band lateral on stipes, a state shared with less derived *Diacheila*. However, I failed to show if *Neoelaphrus* is ancestral to *Arctelaphrus*, or shares a recent ancestor with *Arctelaphrus* or with the remaining subgenera.

The larvae of *Neoelaphrus* are arranged in two groups: the *fuliginosus* and the *cupreus* group. The ancestor of the fuliginosus group evolved a very pale parietale, increased the number of accessory setae especially on the disc of mesonotum, metanotum and abdominal terga, acquired a shorter epicranial suture, and lost the pointed sculpture from dorso-lateral surface of parietale. I failed to show the naturalness of the cupreus group.

4.5 Convergence

Not all character states are unique or evolutionarily unreversed. It is important to recognize these convergent similarities. Ball (1975) points out their importance as clues to major selective forces at work on members of a genus. In reconstruction, I used a few of these characteristics.

In my analysis of relationships exhibited by adult features, the following character states evolved more than once: abdominal sterna 3 and 4 without setae--twice; disc of prosternum without setae, intercoxal process of mesosternum without setae, lateral ridge of mesosternum absent, metasternal lateral setae absent--three times each; parameres of male genitalia with short setae--at least three times; midtibial apico--internal point in males absent--four times.

In my analysis of relationships exhibited by larval features, the following character states evolved twice:

nasale teeth absent; short head; lateral surface of stipes completely sclerotized; extremely small lacinial seta; eight to 10 accessory setae on disc of mesonotum; small internal seta of internal poststernites; pointed sculpture on 5% of disc of terga 4 and 5; pointed sculpture on urogomphus absent.

In my analysis of relationships among adults of species of the Elaphrus subgenus Neoelaphrus, the following character states were evolved more than once: Abdominal sterna 5 and 6 without accessory setae, apex of median lobe of male genitalia wide and twisted, dorsal puncture density, 10 to 30 microns apart, 10 to 200 microns apart, brilliant green upper surface, pronotum with one discal impression, narrow apex of median lobe, in lateral view--twice each; meshes of microsculpture very restricted on elytra, indistinct mirrors on elytra--three times each.

Table 30. Distibution of characteristics of adults among genera and subgenera and of coded character states. (Code explained in section 4.1.1.) (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

			Taxa			
	D	B	A	N	E	Et
Characteristics						
Eye shape:						
small, 0						
typical, 0.5						
prominent, 1.0	0.25	0.5	1	1	1	1
thickness, cornea:						
similar, 0						
thinner ant., 1.0	0	0	0	0	1	1
Head, punctures distribution:						
restricted or absent, 0						
on all of disc, 1.0	1	0	1	1	1	1
Antennae, proportions, antennomeres 1:2:						
2x longer, 0						
1.5 to 1.7x longer, 1.0	0	0	1	1	1	1
Mandible, right, retinacular basal tooth:						
single, 0						
double, 1.0	0	0	1	1	0	0
retinacular apical tooth:						
near terebral tooth, 0						
distant, 1.0	1	0	1	1	0	0
Maxillary, proportions palpomeres 3:4:						
0.67, 0						
0.5, 0.5						
0.3, 1.0	0	0.5	0.5	1	1	1
lacinia, teeth size:						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
Labium, proportion, palpomeres 1:2:						
0.5, 0						
0.7-0.8, 1.0	1	0	1	1	1	1
Mentum, no. setae:						
2, 0						
4, 1.0	0	1	0	0	0	0
Gula, no. setae:						
8, 0						
6, 1.0	0	0	0	0	0	1

Table 30 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

	Taxa					
Characteristics	D	B	A	N	E	Et
Thorax, pronotum,						
no. lateral setae:						
2, 0						
1, 1.0	0	0	1	1	1	1
no. discal impressions:						
0, 0						
1 or more, 1.0	0	0	1	1	1	1
lateral bead:						
complete, 0						
incomplete (sinuation), 0.5						
absent, 1.0	0	0	0.5	0.75	1	1
posterior fringe, termination from postero-lateral angle:						
before lat. impr., 0						
in lat. impr., 0.5						
at angle, 1.0	0	0.5	0.5	0.75	1	1
fringe, seta shape:						
narrow, 0						
scimitar, 0.5						
wide scimitar, 1.0	0.5	0	0.5	0.5	1	0.5
punctures distribution, disc:						
very restricted, 0						
on all of disc, 1.0	1	0	1	1	1	1
Proepisternum, suture epist. and epim.:						
distinct, 0						
indistinct, 1.0	0.5	0	0	0	1	1
ridge, epist. and flange:						
complete, 0						
0.5 complete, 0.5						
0.05 complete, 1.0	0.5	0	1	1	1	1
flange size:						
small, 0						
medium, 0.5						
large, 1.0	0	0	0.5	1	1	1
Prosternum, lat. margin shape:						
angulate, 0						
sinuate, 1.0	0	0	0	1	0	0

Table 30 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

			Taxa			
Characteristics	D	B	A	N	E	Et
ant. fringe, seta shape:						
narrow, 0						
narrow + scimitar, 0.33						
scimitar, 0.67						
wide scimitar, 1.0	0.33	0	0.67	0.67	1	0.67
disc, setae distribution:						
absent, 0						
intercoxal process, 0.5						
covering disc, 1.0	0	0	1	0.25	1	0.25
pointed sculpture, coxal cavity:						
small points, 0						
large points, 1.0	0	0	1	1	1	1
Scutellum, basal ridge:						
present, 0						
absent, 1.0	1	0	1	1	1	1
punctures:						
present, 0						
absent, 1.0	0	1	0	0	0	0
Mesepisternum, anterior submedial ridge:						
distinct, 0						
absent or indistinct, 1.0	0.5	0	1	1	1	1
Mesosternum, lateral ridge:						
distinct, 0						
indistinct, 0.5						
absent, 1.0	1	0	0.5	0.5	1	1
Mesosternum, intercoxal process, setae:						
absent, 0						
present, 1.0	0	0	0	0	1	0.5
Metanotum size apico-lateral setae:						
large, 0						
small, 1.0	1	0	1	1	1	1
Metepisternum, ant. ridge:						
convex ridge, 0						
ridge distinct, 0.5						
absent, 1.0	0.25	0	0.5	0.5	1	1

Table 30 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

			Taxa			
	D	B	A	N	E	Et
Characteristics						
Metasternum, ant. acc. setae:						
present, 0						
absent, 1.0	1	1	0	0	0	0
lateral setae:						
present, 0						
absent, 1.0	1	1	0	1	0	0.5
Abdomen, terga						
setae, tergum 1:						
absent, 0						
present, 1.0	0	1	0	0	0	0
ant. submedial ridges						
tergum 2:						
absent, 0						
present, 1.0	0	0	1	1	1	1
stridulatory scraper,						
points density:						
20 microns apart, 0						
30-40 microns apart, 1.0	1	0	0	0	0	0
microsculpture, tergum 8:						
absent, 0						
present, 1.0	0.5	0	1	1	1	1
Sterna 3-4, medial acc. setae:						
absent, 0						
present, 1.0	0	0.5	1	1	1	1
apical setae, sternum 7:						
2, 0						
4, 1.0	0	1	1	1	1	0.5
puncture distribution:						
sternum 2, 0						
sterna 2-4, 0.5						
sterna 2-6, 1.0	0.5	0	1	1	1	1
Elytra, striae, disc:						
distinct, 0						
indistinct, 0.5						
absent, 1.0	0	0	0.5	0.5	1	1
transverse basal stria:						
complete, 0						
terminated at stria 5, 0.5						
terminated at shoulder, 1.0	0.75	0.25	1	1	1	1

Table 30 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

	Taxa					
Characteristics	D	B	A	N	E	Et
stria 5, base:						
indistinctly impressed, 0						
deeply impressed, 1.0	0.5	0	1	1	1	1
setigerous punctures,						
no. discal rows						
1, 0						
2, 0.5						
3, 1.0	0	0.5	1	1	1	1
size:						
20 microns, 0						
30 microns, 0.5						
40-60 microns, 1.0	0	0	0.5	1	1	1
interval 3:						
entire, 0						
catenate, 0.5						
catenation mirror-like, 1.0	0	0.5	1	1	1	1
pits, ridges:						
absent, 0						
narrow, 0.5						
wide, 1.0	0	0	1	0.75	0	0
punctures:						
absent, 0						
3-25, 0.33						
30-50, 0.67						
50 or more, 1.0	0	0	0.33	0.33	1	0.67
intervals 4, 6 and 8,						
punctures:						
present, 0						
absent, 1.0	1	1	0	0	0	0
micropores in punctures:						
few, 0						
regular, 0.5						
common, 1.0	0	0	1	1	0	0.5
elytral articulation,						
no. elongate punctures:						
5-7, 0						
2-4, 1.0	0	0	0	0	1	1
elytral epipleuron,						
punctures:						
absent, 0						
present, 1.0	1	0	1	1	1	1

Table 30 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

	Taxa					
Characteristics	D	B	A	N	E	Et
Legs, foreleg, coxa,						
punctures:						
absent, 0						
present, 1.0	1	0	1	1	1	1
trochanter, no. setae:						
1, 0						
2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
Femur, no. setae:						
10-25, 0						
30-60, 0.5						
60-80, 1.0	0	0	1	0.5	1	0.5
Tibia, male, no. setae:						
15-27, 0						
30-45, 1.0	0	0	0.5	1	1	0.5
fringe, basal setae:						
4-8, 0						
absent, 1.0	0	0	0	1	1	1
setae no., postero-medial						
row, male:female:						
similar, 0						
dissimilar, 1.0	0	0	0	0	1	1
tarsomere, male,						
no. enlarged:						
4, 0						
3, 1.0	0	0	0	0	1	1
Midleg, coxa punctures:						
absent, 0						
present, 1.0	0.5	0	1	1	1	0.5
setae no.:						
1 or 2, 0						
numerous, 1.0	0	0	1	1	1	1
trochanter, setae no.:						
absent, 0						
1 or 2, 0.5						
3, 1.0	0.5	0	0.5	0.5	1	0.5
femur, setae no.:						
30-45, 0						
80-110, 1.0	0	0	1	0.5	1	0.5
antero-medial row apex:						
expanded, 0						
linear, 1.0	0	0	1	1	1	1

Table 30 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

			Taxa			
Characteristics	D	B	A	N	E	Et
Hind leg, coxa punctures:						
present, 0						
absent, 1.0	0.5	1	0	0	0	0
coxa, setae no.:						
2, 0						
3, 0.33						
3-15, 0.67						
30-40, 1.0	0.33	0	0.67	0.5	1	0.67
trochanter, spinules no.:						
4-6, 0						
10-15, 1.0	0	1	0	0	0	0
femur, setae no.:						
1-4, 0						
5-10, 0.5						
15-30, 1.0	0	0	1	0.5	1	1
tibia, external row:						
absent, 0						
present, 1.0	0	0	1	1	1	1
antero-medial row apex:						
expanded, 0						
linear, 1.0	0	0	1	1	1	1
Male genitalia, median lobe						
baso-dorsal:						
open, 0						
closed, 1.0	1	0	0	0	0	0
stylet, base:						
narrow, 0						
enlarged, 1.0	0	1	1	1	1	1
apico-ventral point:						
present, 0						
absent, 1.0	1	0	1	1	1	1
parameres, width,						
right:left:						
0.75, 0						
0.50-0.3, 1.0	0	0	0	0	1	1
Ovipositor, stylus,						
basal sclerite, setae:						
apical 0.67, 0						
apical 0.25, 0.33						
apical 0.1, 0.67						
absent, 1.0	0.5	0	0.67	0.33	1	1

Table 30 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

	Taxa					
Characteristics	D	B	A	N	E	Et
ridge:						
present, 0						
absent, 1.0	0	1	0	0	0	0
apical sclerite, disc,						
setae no.:						
many, 0						
few (4-6), 0.5						
absent, 1.0	0.5	0	0.5	0.5	0.5	1
setae size:						
absent, 0						
fine, 0.5						
stout, 1.0	0.5	0.5	1	1	1	0
apical setae, no. and size,:						
2 small, 0						
2 very small, 0.33						
1 very small, 0.67						
absent, 1.0	0	0	0.33	0.67	1	1

Table 31. Distribution of characteristics of larvae among genera and subgenera and of coded character states. (Code explained in section 4.1.1.) (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
Head, frontale, nasale, medial point:							
slightly prominent, 0							
prominent, 0.33							
very prominent, 0.67							
extr. prominent, 1.0	1-3	0	0.33	0.67	0.67	1	1
teeth distribution:							
united, 0							
separated, 0.33							
very separated, 0.67							
extr. separated, 1.0	1-3	0.16	0	0.33	0.33	1	0.67
teeth size:							
absent, 0							
very small, 0.25							
small, 0.5							
large, 0.75							
very large, 1.0	1	0.5	1	0.75	0.37	0.12	0.05
very small, 0							
small, 0.33							
large 0.67							
very large, 1.0	2-3	0.33	1	0.67	0.67	0	0.33
Position							
seta MMP-E:egg-bursters:							
internal, 0							
external, 1.0	1	0	1	1	1	0	0
pore MA-I:seta MMA:							
internal, 0							
parallel, 1.0	1	0	1	1	1	0	0
seta size, EA-E:							
small, 0							
medium-small, 1.0	1-3	0	1	0	0	0	0.25
EM-P:							
virtually absent, 0							
small, 1.0	1-3	0	1	0	0	0	0
MP:							
virtually absent, 0							
small or larger, 1.0	1-3	0	1	0	0	0	0
Accessory setae size:							
absent, 0							
small, 1.0	2-3	0	1	0	0	0	0

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
		D	B	A	N	E	Et
Characteristics	Stage						
Microsculpture							
antero-medially:							
absent, 0							
present, 1.0	2-3	0	1	0	0	0	0
Parietale shape:							
elongate, 0							
short, 1.0	1-3	1	0	0	0	1	1
occipital suture:							
0.6-1.2 scape l., 0							
0.2-0.6 scape l., 1.0	1	0	0	0	0	1	1
position:							
pore DI-P							
140-160°, 0							
120-130°, 0.5							
90-120°, 1.0	1-3	0	0	0.5	0.5	1	1
seta DI-A:							
post. to post.-lat. angle, 0							
level with angle, 1.0	1-3	0	0	0	0	1	1
seta DMM-P							
level with post.-lat. angle, 0							
anterior, 1.0	1-3	0	0	0	0	1	1
seta VEM-P:setae DEP and VEP-P:							
distant, 0							
moderate, 0.5							
close, 1.0	1-3	0.75	0.25	0.5	0.5	0.9	1.0
pore VEM-A:seta VEM-P:							
distant, 0							
close, 1.0	1-3	0	0	1	1	1	1
pore VEP-A:seta VEP-P:							
external, 0							
internal, 1.0	1-3	0	0	1	1	1	1

Table 31 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

				Taxa			
Characteristics	Stage	D	B	A	N	E	Et
basic seta size, DI-A:							
small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
DMP-A:							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0.5	0.5
very small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
DEP:							
very small, 0							
medium, 0.33							
large, 0.67							
very large, 1.0	1-3	0	1	0.33	0.67	0.33	0.33
VMA:							
small, 0							
medium, 0.5							
large, 1.0	1	0	1	0.5	0.5	0	0
small, 0							
medium, 1.0	2-3	0	1	1	1	1	1
VEP-A:							
medium, 0							
very large, 1.0	1-3	0	1	0	0	0	0
VEM-P:							
small, 0							
medium, 0.5							
large, 1.0	1-3	0	1	0.5	0.5	0.5	0.5
VEP-P:							
medium, 0							
large, 0.5							
very large, 1.0	1-3	0	1	0.5	0.5	0	0
no. accessory setae							
near DMM system:							
0-5, 0							
7-9, 1.0	2	0	1	1	1	0	1
lateral surface:							
3-4, 0							
5-6, 0.5							
7-9, 1.0	2	0	1	0	0	0	0.5

Table 31 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
accessory setae size, between DMM-P and DI-A absent, 0 small, 1.0	2-3	0	1	0	0	0	0
microsculpture dorso-laterally: absent, 0 lateral, 0.33 on most, 0.67 on all, 1.0	1	0	1	0.5	1	0.33	0.5
absent, 0 lateral, 0.5 on all, 1.0	2	0	1	1	0	0	0.25
latero-ventrally: absent, 0 latero-basal, 0.5 lateral, 1.0	1	0	1	1	0.75	0.5	0.75
pointed sculpture dorso-laterally: 0%, 0 1-10%, 0.33 15-30%, 0.67 70%, 1.0	2	0	0.33	1	0.5	0.33	0.5
latero-ventrally: absent, 0 1-5%, 0.5 0-30%, 1.0	1	0	0	0	0.75	0	0.75
absent, 0 3-5%, 1.0	2-3	0	0	0	0.5	0	0.5
Antennae, proportion, antennomeres 1:2: 1.5, 0 1.0. 1.0	1	1	0	1	1	1	1
Mandibles, base width: narrow, 0 wide, 1.0	1-3	0	0	1	1	1	1
Maxillary stipes, proportion, ventral view: short, 0 medium, 0.5 long, 1.0	1-3	0	1	0	0.5	0	0

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
lateral surface,: sclerotized, 0 with unsclerotized band, 0.5 unsclerotized band extruded, 1.0	1-3	0.5	0	0.5	0	0.5	1
position, interno-basal pore: distant, 0 close, 1.0	1-3	1	0	0	0	1	1
antero-external seta vs lacinia: posterior, 0 anterior, 1.0	1-3	1	1	0	0	0	0
seta size, antero-internal: small, 0 medium, 1.0	2-3	1	0	0	0	0	0
no. accessory setae, postero-external: absent, 0 present, 1.0	2	0	1	0	0	0	0
internal 0.5, dorsum: 20-30, 0 40-50, 1.0	1-3	0	0	0	0	0	1
no. rows in apical 0.3: 1, 0 2, 0.5 3 or more, 1.0	1-3	0	0	0	0	0.5	0.75
Lacinia, shape: conical, 0 suggested, 1.0	1-3	0	0	1	1	1	1
basic seta size, extremely small, 0 small, 1.0	1-3	0.5	0	1	1	1	1
Galea, galeomere 2 position, internal microseta: apical 0.6-0.8, 0 apical 0.6-0.4, 0.5 apical 0.3-0.1, 1.0	1-3	0.5	0	0.5	0.5	1	1

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
galeomere 2,							
size basic seta:							
virtually absent, 0							
very small, 0.5							
small or larger, 1.0	1-3	0	0.5	0.5	0.5	1	1
Maxillary palpi,							
proportion,							
palpomeres 1:2:							
1.5, 0							
1.0, 1.0	1	0	0	0	0	1	1
Labium, ligula size:							
wider, 0							
narrower, 1.0	1-3	0	0	1	1	1	1
basic seta size,							
antero-dorsal:							
small or smaller, 0							
medium-small, 1.0	1	0	0	0	0	0	1
very small, 0							
small, 1.0	2-3	0	1	1	1	1	1
no. accessory setae,							
dorso-laterally:							
2, 0							
5-6, 0.5							
9-15, 1.0	2	0	1	0	0.5	0.5	1
accessory setae size,							
baso-laterally:							
small, 0							
medium, 1.0	2	0	1	1	1	1	1
Thorax, pronotum,							
basic seta size, MI:							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0	1	0	0.5
ME-I:							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0	1	1	0.5
PII-P:							
very small, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0.5	1	0	0.5

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
no. accessory setae							
disc:							
5, 0							
15-20, 0.33							
25-50, 0.67							
90 or more, 1 .0	2	0	1	0.33	0.33	0.33	0.67
epipleuron:							
1, 0							
2, 0.33							
3, 0.67							
12-14, 1.0	2	0	1	0.1	0.4	0.1	0.2
accessory setae size,							
posterior row:							
absent, 0							
small, 1.0	2-3	0	1	1	1	1	1
epipleuron:							
absent, 0							
very small, 0.33							
medium-small, 0.67							
medium-large, 1.0	2	0	1	0.33	0.67	0.5	0.5
microsculpture, disc:							
absent, 0							
5-20%, 0.33							
60%, 0.67							
100%, 1.0	1	0	0.33	0.67	0.16	1	0.67
absent, 0							
10-75%, 0.5							
100%, 1.0	2	0	0.5	1	0.25	1	0.5
pointed sculpture, disc:							
absent, 0							
3-5%, 1.0	1	0	0.5	0	0	1	0
Episternum,							
size basic setae:							
very small, 0							
small, 0.5							
medium, 1.0	1	0	1	0.5	0.5	0	0.5
accessory setae							
small, 0							
medium, 1.0	2	0	1	0	0	0	0

Table 31 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

				Taxa			
Characteristics	Stage	D	B	A	N	E	Et
Epimeron,							
size basic setae:							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0.5	0.5	0.5	0.5
no. accessory setae:							
1, 0							
5-7, 1.0	2	0	1	0	0	0	0
sternite,							
no. accessory setae:							
2, 0							
10, 1.0	2	0	1	0	0	0	0
Mesonotum,							
size basic setae,							
PIM-I and PIE-A:							
medium, 0							
large, 1.0	1-3	1	1	1	1	0	0
PII-P							
absent, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0.5	1	0.5	0.5
no. accessory setae:							
disc:							
8, 0							
15-20, 0.33							
40, 0.67							
60-80, 1.0	2	0	1	0.33	0.33	0	0.5
epipleuron:							
1-2, 0							
4-5, 0.5							
7-13, 1.0	2	0	1	0	0.25	0	0.25
accessory setae size,							
posterior row:							
absent, 0							
small, 1.0	2	0	1	1	1	0.75	0.5
microsculpture, disc:							
10-50%, 0							
60-70%, 1.0	1	0	0	1	0	1	1
0-5%, 0							
20-40%, 0.5							
90-100%, 1.0	2	0	0.5	1	0.5	1	1

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
pointed sculpture,							
disc laterally:							
5-15%, 0							
25-35%, 1.0	1	0	0	0	0	1	0.5
anterior band,							
absent, 0							
30-50%, 0.5							
100%, 1.0	2	0	0.25	0	0	0.5	1
posterior band							
absent, 0							
30-50%, 0.5							
100%, 1.0	1-3	0	0	0	0.25	0.5	1
Anterior pleurite							
basic seta size:							
very small, 0							
medium, 1.0	2	0	1	0	0	0	0
Epipleuron,							
basic seta size:							
small, 0							
medium, 0.5							
very large, 1.0	1	0.5	1	0.5	0.5	0	0.5
medium-small, 0							
large, 1.0	2-3	0	1	0	0.5	0	0
no. accessory setae:							
1-3, 0							
9-16, 1.0	2	0	1	0	0.5	0	0
accessory setae size:							
absent, 0							
very small, 0.5							
medium-small, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
microsculpture:							
absent, 0							
single-pointed, 1.0	2-3	0	0	0	0	0	1
Episternum,							
no. accessory setae:							
1, 0							
3-6, 1.0	2	0	1	0	0	0	0
Epimeron,							
no. accessory setae:							
1, 0							
4-10, 1.0	2	0	1	0.5	0	0	0

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
Anterior sternite,							
basic seta size:							
absent, 0							
very small, 1.0	1	0	1	1	1	1	1
absent, 0							
small, 0.5							
medium, 1.0	2-3	0	1	0.5	0.5	0.5	0.5
no. accessory setae:							
0, 0							
2-3, 1.0	2	0	1	0	0	0	0
Sternite,							
basic seta size:							
small, 0							
medium, 1.0	1	0	1	1	1	0	1
medium, 1.0	2	0	1	0	0	0	0
no. accessory setae:							
0. 0							
3, 1.0	2	0	1	0	0	0	0
Abdomen, terga,							
basic seta size,							
AII and AIM (1-8):							
medium, 0							
large, 1.0	1	0	1	0	0	0	0
small, 0							
medium, 1.0	2-3	0	1	1	1	1	1
AIM (1-8):							
similar on all, 0							
abruptly smaller, 1.0	1-3	0	0	0	0	1	0
PII-P (1-8):							
very small, 0							
small, 0.5							
medium, 1.0	1-3	0	1	0	0	0	0.5
MPP-E (9)							
absent, 0							
small, 1.0	2-3	0	1	1	0.5	0.5	1
AM-P (10):							
very small, 0							
small, 0.5							
large, 1.0	1	0.5	1	0.5	0.5	0	0.5
small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	0.75	0.5	0.5

Table 31 continued. (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
PI-P (10):							
small, 0							
medium, 0.5							
large, 1.0	2-3	0	1	0.5	1	0.5	0.5
no. accessory setae,							
disc (1-8):							
7-10, 0							
15-20, 0.33							
25-30, 0.67							
40, 1.0	2	0	1	0.33	0.5	0	0.5
urogomphus (9):							
7, 0							
15-25, 1.0	2	0	1	0	0.5	0	0
disc (10):							
absent, 0							
2-3 major, 1.0	2	0	1	0	0.5	0	0
absent, 0							
1 minor, 0.1							
4-5 minor, 0.2							
20 minor, 1.0	2	0.2	1	0.1	0.15	0	0.05
position, acc. setae,							
antero-lateral major:							
lateral, 0							
antero-dorsal, 1.0	2-3	0	0	0	0	1	1
microsculpture, type,							
anterior 0.5, disc:							
single-pointed, 0							
multi-pointed, 1.0	1	1	0	1	1	1	1
disc (2-4):							
absent, 0							
single-pointed, 0.5							
multi-pointed, 1.0	2-3	0	0.25	0	0.5	0.5	1
urogomphus (9):							
scale-like, 0							
single-pointed, 1.0	2-3	0	1	0	1	0	0
pointed sculpture,							
disc (4-5):							
5%, 0							
100%, 1.0	2	0	1	1	0.5	1	1
terga no., restricted:							
1-3, 0							
1-7, 1.0	2	1	0	0	0.5	0	0

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
anterior band (1-8):							
0-5%, 0							
100%, 1.0	1	0	0	0	0	0	1
0%, 0							
50%, 0.5							
100%, 1.0	2	0	0.5	0	0	1	1
anterior band (9):							
0%, 0							
10%, 0.5							
100%, 1.0	2	0	0.5	0	0.25	1	1
Epipleuron, shape (1-8):							
entire, 0							
divided, 1.0	2-3	0	1	0	0	0	0
basic seta size,							
anterior seta:							
medium, 0							
large, 1.0	1-3	0	1	0	0	0	0
anterior seta (1-8):							
similar on all, 0							
abruptly changed, 1.0	1-3	1	0	1	1	1	1
anterior seta (9):							
small, 0							
medium, 1.0	1-3	0	1	0	1	0	0.5
no. accessory setae:							
3-4, 0							
8, 0.33							
12-15, 0.67							
30, 1.0	2	0	0.67	0.33	0.67	0.33	0.5
Hypopleuron (1-8),							
no. accessory setae:							
4-6, 0							
12-16, 0.5							
20, 1.0	2	0	1	0	0.5	0	0.75
accessory setae size,							
major setae:							
medium, 0							
large, 1.0	2	0	0	1	1	1	1
minor setae:							
very small, 0							
small, 0.5							
medium, 1.0	2	0	1	0.5	1	0.5	0.5

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
		D	B	A	N	E	Et
Characteristics	Stage						
Sternite							
no. accessory setae							
(1):							
2-6, 0							
8-16, 1.0	2	0	1	0	0	0	0
(2-7):							
8-20, 0							
30-40, 1.0	2	0	1	0	0	0	0
(8):							
8-15, 0							
20-25, 0.5							
40-45, 1.0	2	0	1	0	0.25	0	0
(9):							
absent, 0							
4-6, 0.5							
16-26, 1.0	2	0	1	0	0	0	0.5
(10), major setae:							
2, 0							
3, 0.5							
5, 1.0	2	0	1	0.5	0.5	0	0
(10), minor setae:							
3-4, 0							
6, 0.5							
14, 1.0	2	0.5	1	0	0.25	0	0.5
microsculpture:							
absent, 0							
15% of (9), 0.5							
30% of (9), 1.0	1	0	1	1	0.5	1	1
(2-9):							
single-pointed, 0							
s. and m. pointed, 0.5							
multi-pointed, 1.0	2-3	0.5	0.5	1	1	0	0
External poststernite,							
no. accessory setae,							
(1):							
1, 0							
2-4, 0.5							
7, 1.0	2	0	1	0.5	0.5	0.5	0.5
(2-7):							
3-4, 0							
7-10, 1.0	2	0	1	0	0.5	0	0

Table 31 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Stage	D	B	A	N	E	Et
Internal poststernite,							
basic int. seta size,							
(1-8):							
very small, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0	0	0	0.5
(9):							
very small, 0							
small, 0.5							
medium-small, 1.0	1-3	0	1	0	0	0	0.5
no. accessory setae,							
(1):							
0-2, 0							
6, 1.0	2	0	1	0	0	0	0
(2-7):							
1-2, 0							
3-4, 1.0	2	0	1	0	0.5	0	0

Table 32. Distribution of selected characteristics of adults among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

		Taxa					
Characteristics	Basis of Judgement	D	B	A	N	E	Et
Clypeus, setae:							
2, a							
4, A	1	a	a	a	a	A	a
Eye convexity:							
typical, b							
very prominent, B	1	b	b	B	B	B	B
Cornea thickness:							
thinner ant., c							
similar, C	1	c	c	c	c	C	C
Frons, lateral sulci:							
straight, d							
octagonal, D	1	d	D	d	d	d	d
Mentum, no. setae:							
2, e							
4, E	1	e	E	e	e	e	e
Submentum, no. setae:							
8, f							
6, F	2	f	f	f	f	f	F
Pronotum, lat. seta:							
2, g							
1 or 0, G	1	g	g	G	G	G	G
lat. margin:							
narrow, h							
explanate, H	1	h	H	h	h	h	h
no. disc impr.:							
absent, i							
1 or more, I	1	i	i	I	I	I	I
post. fringe:							
ended bef. hind angle, j							
ended at hind angle, J	1	j	j	j	j	J	J
Shape fringe setae:							
narrow, scimitar, k							
wide, scimitar, K	2	k	k	k	k	K	k

Table 32 continued: (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

Characteristics	Basis of Judgement			Taxa			
		D	B	A	N	E	Et
Epist.:Epim. suture: distinct, l indistinct, L	1	l	l	l	l	L	L
Prosternum lat. marg.: sinuate, m angulate, M	1	m	m	m	M	m	m
Ant. fringe: 1 type setae, n 2 types setae, N	1	N	n	n	n	n	n
discal setae: present, O absent, O- and o	1-2	o	o	O	O-	O	O-
Scutellum b. ridge: absent, p present, P	1	p	P	p	p	p	p
Mesosternum coxal setae: absent, q or Q- present, Q	1-2	q	q	q	q	Q	Q,Q-
lat. ridge: absent, r or R- present, R	1	r	R	R	r,R-	R-	R-
Metasternum antero-medial setae: absent, s present, S	1	s	s	S	S	S	S
lat. setae: present, T absent, t and T-	1-2	t	t	T	T-	T	T,T-
Abdominal sterna 3-4 accessory setae: absent, u or U- present in males, U on m. and f., U'	1-2	u	U,U-	U'	U'	U'	U'
Elytra setigerous punct.: 15-20 microns, v 30 microns, V 40-50 microns, V'	1	v	v	V	V'	V'	V'
Striae, disc: present, w 7-8 irregular, W1 absent, W2	1	w	W1	W2	W2	W2	W2

Table 32 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

				Taxa			
Characteristics	Basis of Judgement	D	B	A	N	E	Et
striae 2 and 3:							
entire, x							
catenate ant. and post. to setigerous puncture, X							
catenate ant. to setigerous punct., X1							
circle around set. punct. larger, X2	1-2	x	X,X1	X2	X2	X2	X2
Interval, no. rows setigerous punct.:							
3, y							
3, 5 and 7, Y							
3, 5, Y-	1	y	Y-	Y	Y	Y	Y
Intervals, 4, 6 and 8:							
entire, z							
catenate, Z							
cat. mirror-like, Z'	1	z	Z	Z'	Z'	Z'	Z'
Foreleg, trochanter:							
1 seta, AA1							
2 setae, aa							
3 setae, AA2	1	aa	AA1	aa	aa	AA2	aa
tibia, post. fringe:							
4-8 setae, ab							
0 or 1 seta, AB	1	ab	ab	ab	AB	AB	AB
no. setae postero-medial row m. vs. f.:							
similar, ac							
very dissimilar, AC	2	ac	ac	ac	ac	AC	AC
no. enlarged male tarsomeres:							
4, ad							
3, AD	1	ad	ad	ad	ad	AD	AD
Midleg, coxa no. setae:							
1 or 2, ae							
numerous, AE	1	ae	ae	AE	AE	AE	AE
trochanter no. setae:							
0, AF1							
1 or 2, af							
3, AF2	1	af	AF1	af	af	AF2	af

Table 32 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

Characteristics	Basis of Judgement	Taxa D	 B	 A	 N	 E	 Et
tibia, male apico-internal point absent, ag or AG- present, AG AG*=AG,AG-	1-2	ag	AG*	AG*	AG*	AG	AG*
Hind leg, coxa extention, setae: absent, ah inner 0.5, AH on all, AH'	1	ah	ah	AH	AH	AH'	AH
Femur, no. setae: 5 or less, ai 20 or more, AI 6 or 12, AI-	1-2	ai	ai	AI	AI-	AI	AI
Microsculpture, dorsum: alveolae flat to subconvex, aj alveolae convex, AJ	2	aj	aj	AJ	aj	aj	aj
Male genitalia, median lobe, baso-dorsal surface: closed, ak open, AK	1	ak	AK	AK	AK	AK	AK
med. lobe, stylet post.: narrow, al enlarged, AL	1	al	AL	AL	AL	AL	AL
dorsum, right apexap1025':' smooth, am lat. point, AM	1-2	am	am	AM	am	am	am
Parameres, seta size: - short, an or AN- long, AN	1-2	an	an	an	AN	AN-	AN-
Ovipositor, stylus apical sclerite setae: 2 small, ao 2 very small, AO 1 very small, AO' 0, AO"	1-2	ao	ao	AO	AO'	AO"	AO"

Table 33. Distribution of selected characteristics of larvae among genera and subgenera of Elaphrini and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated as 'D' for Diacheila, 'B' for B Blethisa, 'A' for Arctelaphrus, 'N' for Neoelaphrus, 'E' for Elaphrus and 'Et' for Elaphroterus.)

			Taxa					
			D	B	A	N	E	Et
Characteristics	Stage	Expl.						
Head, color: yellow and brown, a orange, A	1-3	1	a	a	A	a	a	a
Nasale								
med. projection: short, b long, B very long B' extr. long, B"	1-3	1	b	B	B'	B'	B"	B"
projection, apex: single-pointed, c 3-pointed, C	1-2	1	C	c	c	c	c	c
teeth, position: lateral, d medial, D	1-2	1	d	D	d	d	d	d
teeth size: small, e or E3 very small to absent, E1 large, E2	2	1	e	E2	E2	E2	E1	E3
Parietale								
occipital suture: 1.0-1.2 scape length, f 0.2-0.6 scape length, F	2-3	1	f	f	f	f	F	F
length: long head, g short head, G	1-3	1	G	g	g	g	G	G
Pore VEP-A, position: int. to VEP-P, h ext. to VEP-P, H	1-3	1	h	h	H	H	H	H
Mandible, base width: narrow, i wide, I	1-3	1	i	i	I	I	I	I

Table 33 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

			Taxa					
Characteristics	Stage	Expl.	D	B	A	N	E	Et
Stipes ext. surface: sclerotized, J2 narrow unscl. band, j unscl. band + bump, J1	2-3	2	j	J2	j	J2	J1	J1
int. brush, no. rows: 1 apical 0.33, k 2-3, K	1-3	1	k	k	k	k	K	K
acc. setae, external surface: absent, l present, L	2-3	1	l	L	l	l	l	l
Galeomere 1, seta virtually absent, m v. small M	1-3	1	m	M	M	M	M	M
Lacinia, shape: coniform, n suggested, N	1-3	1	n	n	N	N	N	N
seta size: small, o extr. small, O	1-3	1	o,O	O	o	o	o	o
Pronotum, disc accessory setae: 4-5, p 10-20, P 30-40, P1 90 or more, P2	2	1	p	P2	P	P	P	P1
Pronotal epipleuron accessory setae: 0, q 2-3, Q 5-7, Q1 12-14, Q2	2	1	q	Q2	Q	Q,Q1	Q	Q
Mesonotum, disc no. acc. setae: 8-10, r or R4 12-15, R1 20-40, R2 60-70, R3	2	1-2	r	R3	R4	R1	R4	R2

Table 33 continued. (Taxa abbreviated as 'D' for *Diacheila*, 'B' for B *Blethisa*, 'A' for *Arctelaphrus*, 'N' for *Neoelaphrus*, 'E' for *Elaphrus* and 'Et' for *Elaphroterus*.)

			Taxa					
Characteristics	Stage	Expl.	D	B	A	N	E	Et
Abdomen, terga 1-8 seta AIM size: similar on 1-8, s abruptly smaller, S	1-2	1-2	s	s	s	s	S	s
Epipleuron, size anterior seta: small, t medium-small, T	1-3	1-2	t	t	t	T	t	t
Sternites, 2-7 no. acc. setae: 14-25, u 30-40, U1 90-150, U2	3	1-2	u	U2	u	u	u	U1
Internal poststernite, int. seta size 1-8: very small, v small, V	1-3	2	v	V	v	v	v	V
Microsculpture, extension, nota: restricted or absent, w widespread, W	1-3	1	w	w	W	w	W	W
Pointed sculpture, terga 4-5: on all of disc, x 5% of disc, X	2	1	X	x	x,X	x	x	x
Urogomphus: single-pointed, y scale-like, Y absent, Y'	1-3	1	y	Y	Y'	Y,Y'	y	y
sternite 9: no meshes, z meshes distinct, Z	3	1	z	z	Z	z	z	z

Table 34. Distribution of selected characteristics of adults among groups of subgenus Neoelaphrus and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated 'u' for uliginosus, 'f' for fuliginosus, and 'c' for cupreus.)

		Taxon groups		
Characteristics	Explanation	u	f	c
Eye, cornea thickness:				
40-60 microns, a				
100 microns, A	1	a	A	a
Pronotum, lateral bead:				
thick, 20-30 microns, b				
thin, 10-15 microns, B1				
absent, B2	1	b	b,B2	B1
lateral margin, lat. view:				
straight, c				
sinuate at middle, C	1-2	C	c	c
termination of post. fringe:				
40-120 microns from hind angle, d				
150-200 microns, D				
200-250 microns, D'	1	d	D,D'	D'
disc, antero-submedial impr.:				
absent, e				
present, E	1	E,e	e	e
Abdomen, sterna 5 and 6 accessory setae:				
present, f				
absent, F or F-	2	f	F	f,F-
Foreleg, males, base post. spur:				
without large point, g				
with large point, G	1	g	G	g
Punctures, surrounding surface of pleura:				
narrowly or not depressed, h				
widely depressed (80 microns), H	1	h	H	h
size, pleura:				
30-45 microns, i				
20-30 microns, I	1	i	i	I
Male genitalia, apex median lobe lateral view:				
narrow, j				
wide, J1				
very wide, J2	1	j	J1	J2,j

Table 35. Distribution of selected characteristics of adults among species of *uliginosus* group and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated 's' for *splendidus*, 'j' for *japonicus*, 'u' for *uliginosus*, 'p' for *pyrenaeus*.)

		Taxon groups			
Characteristics	Explanation	s	j	u	p
Dorsum, color: Green, k brilliant green, K brown copper, K1	1	K	K1	k	K1
Color of elytral pits: purple metallic, l green metallic, L	1-2	L	l	l	l
Pronotum, antero-lateral impr.: absent, m present, M	1	m	M	M	M
Elytra, sutural mirrors: flat and distinct, n convex and distinct, N1 flat and indistinct, N2	1	N1	n	n	N2
no. rows mirrors: 2, o 4, O	1	O	o	o	o
Hind leg, coxa, no. setae: 3-7, p 8-15, P	1	P	p	p	p
Punctures, density pronotum:elytra: similar, q dissimilar, Q	1	Q	q	q	q
intervals 4, 6 and 8 30-40 microns apart, r 100-150 microns apart, R1	1	r	R1	r	r
Microsculpture meshes: widespread, s very restricted, S	1-2	S	s	s	S
Male genitalia, apex median lobe, dorsal view narrow + straight (20-30 microns), t wide + twisted, (60-65 microns), T	1	t	t	T	T
Male genitalia, apex median lobe, lateral view: narrow, j enlarged ventrally, J3	1	j	J3	j	j

Table 36. Distribution of selected characteristics of adults among species of the fuliginosus group and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated 'f' for fuliginosus, 'l' for lindrothi , 'c' for cicatricosus.)

		Taxon groups		
		f	l	c
Characteristics	Explanation			
Color, dorsal:				
green, k				
very dark copper, K2				
silvery-brass, K3	1	k	K3	K2
Color, tarsomeres:				
purple, u				
green, U	2	U	u	u
Pronotum, lateral bead:				
thick (20-30 microns), b				
absent, B2	1	b	B2	B2
Termination of post. fringe:				
150-200 microns to hind angle, D				
200-250 microns to hind angle, D'	1	D	D'	D'
Abdomen, sternum 7, males, accessory setae:				
present, v				
absent, V	1	v	V	V
Elytra, sutural mirrors:				
distinct and flat, n				
indistinct and flat, N2	1	n	N2	n
Foreleg, trochanter, setae:				
2, w				
1, W	1	w	w	W
Punctures, density, intervals 4, 6 and 8:				
30-40 microns, r				
10-200 microns, R2				
10-30 microns, R3	1-2	r	R3	R2

Table 37. Distribution of selected characteristics of adults among species of the *cupreus* group and evolutionary classification of the character states. (Code explained in section 4.1.2.) (Taxa abbreviated as 's' for *sibiricus*, 'cu' for *cupreus*, 'cl' for *clairvillei*, 'o' for *olivaceus*, and 'l' for *laevigatus*.)

		Taxon groups				
		s	cu	cl	o	l
Characteristics	Expl.					
Color, dorsum:						
green, k						
dark copper, K4						
black, K5	1	k	K4	k	k	K5
Pronotum, discal impressions:						
2, x						
1, X	1	x	x	X	x	X
Prosternum, intercoxal process:						
with setae, y						
without setae, Y	1	y	y	y	Y	Y
Abdomen, sterna 5 and 6:						
with accessory setae, f						
without, F-	1	f	f	f	F-	f
Abdomen, sternum 7, males:						
with accessory setae, v						
without, V	1	v	v	v	V	v
Elytra, mirrors:						
distinct, n						
indistinct, N2	1	n	n	N2	N2	N2
pits, lateral ridges:						
separated, z						
fused, Z	1	z	z	Z	Z	Z
setigerous punctures:						
distinct, aa						
indistinct, AA	1	aa	aa	aa	aa	AA
Midleg, tibia, apico-internal points:						
present, ab						
absent, AB	1	ab	ab	ab	AB	AB
Punctures, size, dorsum:						
20-30 microns, ac						
10-20 microns, AC	1	ac	ac	ac	AC	AC
density, pleuron:						
30-40 microns apart, ad						
10-20 microns apart, AD	1-2	ad	ad	ad	AD	AD

Table 37 continued. (Taxa abbreviated as 's' for sibiricus, 'cu' for cupreus, 'cl' for clairvillei, 'o' for olivaceus, and 'l' for laevigatus.)

		Taxa				
		s	cu	cl	o	l
Characteristics	Expl.					
density, intervals						
4, 6 and 8:						
30-40 microns apart, r						
10-20 microns apart, R4						
10-200 microns apart, R5						
200 microns or more, R6						
50-100 microns apart, R7	1	r	R7	R5	R4	R6
density, metasternum,						
antero-medially:						
50-100 microns apart, ae						
20 microns apart, AE	1	ae	ae	ae	AE	ae
no. in pits,						
8-15, af						
3-5, AF	1	af	af	af	af	AF
Microsculpture meshes, dorsum:						
expanded, s						
very restricted, S	1	s	s	S	S	S
Male genitalia,						
apex med. lobe,						
dorsal view:						
thin and straight (20-30 microns), t						
thick (50 microns) + twisted, T	1	t	t	T	t	t
length of apex						
in dorsal view:						
moderate, ag						
long, AG1						
short, AG2	1	AG1	AG1	ag	AG2	AG2
lateral view:						
narrow, j						
wide, J2	1	J2	J2	j	j	j

5.0 Zoogeography

5.1 Introduction

Elaphrine beetles inhabit temperate and boreal zones of the northern hemisphere, excluding Greenland and Iceland. To reconstruct the past history of the group, I use working principles presented by Darlington (1957), as reviewed by Erwin (1970). Darlington (1957) presented a list of clues which may help determine the probable past history of a group. They are best used in combination, as extinction and recession affect the value of one or more clues.

1. The place of origin may be indicated by the area of greatest diversity. Highly diverse faunas in a given area are probably the result of longer evolutionary history in that area than in other areas where the faunas are much less divergent.
2. The place of origin may be indicated by the area of greatest differentiation. Highly differentiated faunas are probably the result of longer evolutionary history in that area than in other areas where the faunas are much less diverse.
3. The extent of area probably increases with age of the taxon. The older the taxon, the more geological and paleoenvironmental events would allow it to invade previously inaccessible areas.
4. Present geographic and/or climatic distribution of

less derived taxa probably indicate the area of origin and/or the probable climatic zone of the common ancestor.

5. The present distribution of vicariant taxa may indicate area of origin and/or the paleoenvironmental events that brought about these vicariant taxa.
6. Fossils may indicate the area of origin and/or the time scale for the reconstruction of past history of the taxa.

I present first the evidence gathered from extant and fossil specimens. Then I postulate the probable place of origin of elaphrine beetles and then retrace the histories of elaphrine genera and subgenera.

5.1.1 The Evidence

Distribution patterns.- The number of species is nearly equal between Eurasia and North America for elaphrine genera and *Elaphrus* subgenera *Arctelaphrus* and *Neoelaphrus* (Table 38). However, the subgenus *Elaphrus* is more diverse in North America while *Elaphroterus* is more diverse in Eurasia. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group is in Eurasia, the *fuliginosus* group is in North America, and the *cupreus* group is about equally represented in Eurasia and North America.

Within continents, the genera and subgenus *Elaphrus* are

Table 38. Number of extant species of genus-group taxa of Elaphrini confined to or shared between Eurasia and North America.

Taxa	Total	Eurasia	shared	N. America
A. Genera				
Diacheila	3	3	2	2
Blethisa	7	4	2	5
Elaphrus	34	19	4	19
B. Subgenera of Elaphrus				
Arctelaphrus	1	1	1	1
Neoelaphrus	13	7	0	6
Elaphrus	15	7	2	10
Elaphroterus	5	4	1	2
C. Groups of Neoelaphrus				
uliginosus	5	5	0	0
fuliginosus	3	0	0	3
cupreus	5	2	0	3

most diverse on the Pacific side of both land masses (Table 39). However, the only member of Arctelaphrus is Holarctic, the subgenus Neoelaphrus is more diverse in Asia and eastern North America, and Elaphroterus is more diverse in Europe and western North America. The groups of Neoelaphrus are distributed as follows: the uliginosus group is more diverse in Asia, the fuliginosus group is restricted to eastern North America, and the cupreus group is most diverse in Asia and western North America.

Climatic patterns.- In the following discussion, I used broad climatic zones. These zones are briefly defined as follows. The warm temperate zone is characterized by mild winters and long hot summers, for example, in eastern North America this zone extends from southern Pennsylvania to the Gulf of Mexico. The cold temperate zone is characterized by cold winters and hot summers, for example, in eastern North America this zone extends from northern New England to Quebec City. The Boreal zone is characterized by long cold winters and short cool summers for example, in eastern North America this zone extends from the Gulf of St. Lawrence to the northern treeline. The northern half of the Boreal zone is termed the subarctic zone. I also include as subarctic those species whose ranges extend into the southern edge of the tundra regions. Species of elaphrines are generally widespread in one or more climatic zones, inhabiting an area from the southern edge of the tundra to the southern half of the warm temperate zone (Table 40). None are known from

Table 39. Number and distribution of extant species of genus-group taxa of Elaphrini within Eurasia and North America.

Taxa	Eurasia			N. America		
	Europe	shared	Asia	West	shared	East
A. Genera						
Diacheila	1	1	3	2	1	1
Blethisa	1	1	4	5	3	3
Elaphrus	10	6	14	15	6	10
B. Subgenera of Elaphrus						
Arctelaphrus	1	1	1	1	1	1
Neoelaphrus	3	2	6	3	2	5
Elaphrus	3	2	5	9	3	4
Elaphroterus	3	1	2	2	0	0
C. Groups of Neoelaphrus						
uliginosus	2	1	4	0	0	0
fuliginosus	0	0	0	0	0	3
cupreus	1	1	2	3	2	2

subtropical or tropical zones. Most species live at low elevations, while a few are in the subalpine zone. *Elaphrus* and *Blethisa* are represented in all climatic zones, while the *Diacheila* species are arctic, subarctic or subalpine in distribution. Subgenera of *Elaphrus* range over all climatic zones except for the sole member of *Arctelaphrus* which lives in subarctic regions and montane zones along the Rocky Mountains. The groups of *Neoelaphrus* are distributed as follows: the *uliginosus* group has northern warm temperate, cold temperate, boreal species; the *fuliginosus* group has species extended between the northern half of the warm temperate zone and the cold temperate zone; and the *cupreus* group has species in the cold temperate and boreal zone, and one species restricted to the warm temperate zone.

Centres of endemism.- These are outlined only for species of *Elaphrus*. The sole member of *Arctelaphrus* is holarctic in the subarctic zone. *Neoelaphrus* shows endemism in the following areas: southwestern Europe, central Asia, eastern Asia, Japan, boreal North America, and eastern and western North America. *Elaphrus* has centres in southwestern Europe, central Asia, eastern Asia, California, the southern half of the Great Basin with associated Rocky Mountains, and eastern North America. *Elaphroterus* has centers in middle Europe, eastern Asia, boreal Eurasia, and western North America. Because centers have less than three species and the taxa in these centers diverge little from other centers of other members of the same subgenus, I feel these centers

Table 40. Number and distribution of extant species of genus-group taxa of Elaphrini in climatic/geographic zones.

Taxa	s. tundra	Boreal	Temperate		Montane
			cold	warm	
A. Genera					
Diacheila	2	0	0	0	0
Blethisa	1	3	1	2	1
Elaphrus	6	12	18	12	6
B. Subgenera of Elaphrus					
Arctelaphrus	1	0	0	0	0
Neoelaphrus	0	5	6	6	1
Elaphrus	3	5	8	6	5
Elaphroterus	2	2	4	0	0
C. Groups of Neoelaphrus					
uliginosus	0	1	1	1	2
fuliginosus	0	0	2	3	0
cupreus	0	4	3	1	0

are quite insignificant (except the eastern North American center of the fuliginosus group) and reflect the great dispersal power of specimens of most taxa. However, in some centers taxa are much differentiated and offer important clues in reconstructing past events such as the center of Neoelaphrus in eastern North America.

Diversity in North America.- I present a synopsis only for this continent because it has a varied elaphrine fauna and the distribution patterns are better known to me. The most notable fact is that diversity is high in all regions within the subarctic and the northern half of the warm temperate zone (excluding the foggy, cool, maritime zones on the Pacific coast, Newfoundland, subdesert regions, and most of the Canadian Shield), and is followed by an abrupt decrease beyond these climatic zones. In the north, in the Mackenzie delta, seven species live, although north of the tree line, 70 kilometres away, only two species are known. In Maryland, five species are known; while in Virginia southward, only two are recorded. North of the Mogollon rim, in the American southwest, three species are known, while south of it, in the desert area, only one specimen of one species has been collected. In California near San Francisco, six species are known; while near Los Angeles, only one is known. Elsewhere, over an area of about 500 kilometres square, one can expect between five and nine species. Diversity is slightly higher in western North America. The main centres of diversity are: northern

California, Yukon and western Northwest Territories, Colorado, and extreme northern New England.

Dispersal potential and barriers.- On sunny days, *Elaphrus* beetles fly during their active season. Power and frequency of flight is clearly suggested by the abundance of captures of all known New England species near subalpine and alpine bodies of water on Mount Washington, N. H., Mount Mansfield, Vt., and White Face Mountain, N.Y., although these mountainous areas are not normally occupied. Locality labels, Darlington's observations (personal communication) and my own observations clearly suggest that such individuals ("stragglers") have enough control of their flight to land near rather suitable habitats. Most stragglers of other carabid species on mountains or near lake shores are rarely found in a typical habitat.

Power of flight is also suggested by the number of species with geographical range over 3000 kilometres. Studies of various North American carabid genera show 5% of the micropterus *Evarthrus* (Freitag, 1969) have such ranges; while among typical macropterus carabid genera, 17% of *Schizogenius* (Whitehead, 1972) 19% of *Brachinus* (Erwin, 1969), 20% of *Gynandrotarsus* (Noonan, 1973), and 15% of *Anisotarsus* (Noonan, 1973) species extend that far; and 49% of *Elaphrus* species show as large or larger ranges.

I observed behavior of adults of *E*. *americanus* and *E*. *lecontei* on a clay beach associated with fresh water, while they were in transit between suitable habitats. The adults fed, mated and oviposited before continuing exploration for the right habitat. Therefore, not only are *Elaphrus* powerful fliers, but their dispersal potential is increased, since travelling individuals seek any acceptable approximation of their "preferred" habitat where they fill up with energy by eating and eliminate excess weight by ovipositing.

Habitat diversity.- Data presented here are summarized in Fig. 171. Elaphrine beetles are closely associated with water, except for specimens of *D. polita*. Specimens of *D. arctica* live in marshes of very cold standing water near abundant thin mosses. Specimens of *D. polita* occur on the tundra and under willow litter. The adults show many adaptations for digging--probably an early step toward inhabiting subterranean habitats.

All species of *Blethisa* are associated with cold standing water. One species lives on very thick *Sphagnum* moss carpets; most occur in shade of dense *Carex* vegetation, and some live in places with open mud and low moss carpet. Adults and larvae of the above genera are nocturnal (or at least crepuscular) as far as is known. Members of *Elaphrus* are diurnal. Specimens of the sole species of *Arctelaphrus* live on thick moss carpet of neutral pH in sunny places--the water is very cold below. As far as is known, specimens of *Neoelaphrus* occur near small or large rivers or near standing water. Individuals of most species (except *E. lindrothi*) live on mostly organic soil. *E. lindrothi*).

The habitat of most species has little or no vegetation (except for *E. laevigatus* and some of the habitats of *E. clairvillei*). About half of the species live in sunny areas, others in deep shade. Specimens of subgenus *Elaphrus* occur on surfaces with little or no vegetation in very sunny places. Most members are riparian, but some live near standing water, that is cool, warm, or very warm. Very few species are restricted to beaches with high organic content. Most populations live on silt, clay, or a mixture of these soils. Two species are linked to alkaline waters. As far as is known, populations of all species are active along the lower beach. Populations of species of *Elaphroterus* live on surfaces with little or no vegetation and only along rivers (the habitat of *E. punctatus* is perhaps an exception). The riparian habitats are related to major mountain ranges with snow melt in summer. The habitat is either exposed to the sun, or in deep shade. Specimens of these species, as far as known, live on the middle and upper beaches of river banks.

Fossil evidence.- I studied numerous fragments of *Elaphrus* adults of the following species dating from the last glaciation: *E. lapponicus*, *E. clairvillei*, *E. olivaceus*, *E. parviceps*, *E. americanus*, and *E. californicus*. Specimens of these taxa match extant specimens, and specimens of *E. parviceps* and *E. clairvillei* are assigned to extant geographical races. These conclusions are backed by similar observations made by Matthews (1968, 1975), Coope (1970), and Lindroth (1969). However, Howden (1969) and Whitehead (1976) suggest that divergence occurs in many subtropical and tropical elements with islandic patterns (*sensu* Whitehead, 1976). I also examined a few excellent fragments that are from middle Pliocene (about six million year before present--mybp). Most specimens match extant specimens of *E. riparius* complex (mostly *E. tuberculatus*) while one fragment matches the present *E. sibiricus*. Matthews (1970, 1974a, 1974b, 1976) observed for some specimens of that period, no change or slight but significant change. The samples of Quaternary age suggest that no apparent structural changes have occurred in the past 15,000 years and the older fragments show that little or no structural changes can be recognized even from the Pliocene. Matthews (1970, 1974a, 1974b, and 1976) observed little or no differentiation among other lowland carabids of the same age and place.

Synopsis of past geological and climatic events.- North America and Europe were in contact until the end of the Cretaceous (Dietz and Holden, 1970). Early in the Tertiary, Eurasia was linked with North America by Alaska (Hopkins, 1967). This area is referred to as Beringia.

Epicontinental seas bisected Eurasia and North America in the Late Cretaceous. The importance of epicontinental seas cannot be ignored by students of Cretaceous zoogeography as rightly observed by Howden (1974). In North America the sea extended along a north-south axis east of the Rockies until the end of the Cretaceous (Williams and Stelk, 1975). In Eurasia the sea extended along a north-south axis east of the Urals until the Early Eocene (Hopkins, 1967).

Beringia was an open land bridge from the Paleocene (63 mybp) until the Early Pliocene (12 mybp) (Hopkins, 1967). The sea regressed about 10 million years ago, but it transgressed this land in the Late Pliocene (3.5 mybp) (Hopkins, 1967). The bridge was reopened only for some of the glacial periods.

The climatic reconstruction is taken entirely from Wolfe (1972). The study deals with Alaska, a most crucial area. I also have more confidence in his conclusions about past climate based on his analysis of taxa and leaf physiognomy, than I have in the work of other authors. The climate in the Late Cretaceous and Paleocene times was equitable with subtropical conditions extending into Alaska. Beringia was then as far north as it is today. The temperate zone was probably restricted tc northernmost Canada and central northernmost Siberia. Middle Eocene Alaska was tropical. From then on the climate deteriorated until Pleistocene time. In the Late Eocene the climate was equivalent to the southern half of the present warm temperate zone. In the Early Oligocene, Alaska was subtropical. By the Middle Oligocene, the flora was of cold temperate type, but in the Late Oligocene, it was equivalent to the northern half of the warm temperate zone. In the Early Miocene, Alaska was cold temperate. By the Middle and the Late Miocene, boreal conditions developed in northern

Alaska, while southern Alaska was cold temperate. In the Pliocene, boreal conditions extended over Alaska, and by the Late Pliocene, subarctic conditions developed and along the Bering coast grassland appeared. During the Pleistocene, Alaska alternated between arctic and subarctic conditions.

5.2 Historical Zoogeography

5.2.1 The Habitat of the Ancestral Stock of Elaphrini

As suggested by data in section 5.1.1, I hypothesize that the immediate ancestor of elaphrines was associated with water. However, this may be a new adaptation of this immediate ancestor in the temperate zone. The Melaenini consist of three extant species belonging to genus Melaenus. Little is known about them. Therefore, I have no evidence of the probable habitat of the ancestral stock of the Elaphrini.

5.2.2 The Ancestral Habitats of the Extant Taxa

The ancestral climatic zones.- By comparing climatic zones of less derived species of each higher taxon, one could suggest an hypothesis about the probable climatic tolerance of various ancestors (clue 4). Extant species of Diacheila suggest a relatively recent subarctic ancestor, while those of Blethisa suggest a warm or cool temperate ancestor. The only extant species of Arctelaphrus suggests a recent subarctic ancestor; those of Neoelaphrus and Elaphroterus a northern warm temperate zone ancestor, and those of subgenus Elaphrus probably a cold temperate zone ancestor as most extant species are in this zone (clue 1). (The species relationships of this subgenus are incompletely understood.)

5.2.3 The Center of Origin

I believe the center of origin of extant genera and subgenera of elaphrines was in northernmost central Siberia. The evidence is derived from many of the clues presented in section 5.1. To justify this statement, I first discuss Beringia as a secondary center of radiation in order to establish when elaphrines were there and at what state in their evolution. Then I discuss my reason for choosing northern Siberia as the primary center of radiation.

Beringian center. Present diversity of genera and subgenera of elaphrines between North America and Eurasia is the same. Therefore an earlier corridor-like (Simpson, 1953) bridge must have existed. Diversity is highest on the Pacific side of the continents for genera and subgenera. Therefore it is probable that exchange occurred in that area (clue 1). Differentiation in most genera and subgenera is greatest on the Pacific side of the continents. Therefore most of their evolutionary history occurred there (clue 2).

Less derived elements of extant genera and subgenera suggest that ancestors of Blethisa and Elaphrus were adapted to the northern part of the warm temperate zone. Therefore exchange occurred on a bridge with similar climate (clue 4). The distribution of sister groups among warm temperate Neoelaphrus suggest a close association with the mixed mesophytic forest which evolved in Beringia (clue 5). Finally, Pleistocene and the Late Pliocene fossils of Elaphrus suggest a slow evolutionary rate (clue 6). Therefore, the most probable center of Recent infra subgeneric taxa is Beringia, which was warm temperate as early as the Middle Oligocene (30 mybp), and was a wide land bridge then, and could have served as a corridor for dispersal of terrestrial animals. Therefore, at that time ancestors of Blethisa and of Elaphrus subgenera Neoelaphrus, Elaphrus, and Elaphroterus were probably in existence on Beringia. Less derived ancestors of genus Diacheila and Elaphrus subgenus Arctelaphrus were extant, but present evidence cannot confirm their presence on Beringia.

Siberian Center. Extant taxa suggest that their immediate ancestors were not adapted to the subtropical zone, as no extant species or less derived elements suggest such adaptation. Therefore, the common ancestor was probably adapted to temperate climate (clue 1). Since genera and subgenera were probably evolved by Oligocene times, one must assume that the origin of elaphrines goes back to the Late Cretaceous (clue 2). Therefore, the ancestor of elaphrine genera and subgenera should have originated further north as Beringia was too warm in the Late Cretaceous and the Early Tertiary time. The only suggested temperate zones in the northern hemisphere were in the Canadian arctic islands, Greenland, and northernmost central Siberia. I believe that northern central Siberia was the center.

During late Cretaceous time North America and Eurasia were bisected by north-south epicontinental seas. Therefore, exchange between Asia and Europe or between western North America and eastern North America was minimal. If northern Canada or Greenland was the center of origin, I suspect much exchange would have occurred between Europe and eastern North America as both continents were still broadly connected. Moreover, I suspect elaphrines would show a similar distribution and differentiation pattern to the Ansiodactylina (Noonan, 1973) which are most diverse on the Atlantic side of the continent with different subgenera. Therefore, the Siberian center is more compatible with the evidence. This distribution is more compatible with the probable center of evolution of its sister groups the tropically-adapted Melaenini and mountain-adapted Broscina, most diverse and differentiated in southeast Asia.

5.2.4 Evolution of Habitat Preferences among Elaphrine Genera and Subgenera

As all elaphrines (except specimens of *D. polita*) are associated with water, so too were ancestral elaphrines most probably associated with water (clue 1). I postulate that this ancestor was nocturnal (as adults of less derived *Blethisa* and *Diacheila* are nocturnal or crepuscular) and lived near standing water among moderately short vegetation. This habitat matches quite closely that of *D. arctica* and most extant *Blethisa* species (clue 4). The main evolutionary step was taken by the *Elaphrus* ancestor as it became a diurnal predator still associated with water, and with little vegetation to obscure vision. Since many ancestral elements of *Elaphrus* are associated with moss carpet, I feel it probable that this ancestor first adapted to open mud and mossy habitat near water. Also, since in most *Elaphrus* subgenera less derived species are riparian (except *Arctelaphrus*), I feel this ancestor adapted to slow moving and probably cool streams (clue 4).

The habitat of the less derived *Neoelaphrus* elements fits the above description. However, species of *Neoelaphrus* invaded other niches such as shady habitats with few plants (*E. cupreus*) and even shady flood plains (*E. lindrothi*). Species of the *fuliginosus* group are partly or totally riparian while those of the *cupreus* group have some riparian species and mostly (the *clairvillei* subgroup) standing water species. This adaptation is considered secondary as this habitat became available again after the evolution of the more cold hardy elements of the cupreus group. Adaptation to shady habitat occurred three times (E. cupreus, E. clairvillei, and E. laevigatus).

The common ancestor of species of subgenera Elaphrus and Elaphroterus became adapted to slow moving streams and rivers, and to substrates low in organic matter.

The ancestor of species of subgenus Elaphrus remained adapted to slow streams and rivers but invaded different and finer substrates. The ancestors of two species (E. lecontei and E. lheritieri) adapted to standing alkaline waters of ponds and lakes. The ancestor of E. viridis became adapted to dry and wet season cycles.

5.2.5 Past History of the Genus Elaphrus Fabricius

The sister groups of elaphrines are probably the Broscina and the Melaenini. The Broscina are diverse in the mountains of Asia, in Australia and New Zealand. The last derived elements are in Asia. The past history of the Melaenini is unclear as the tribe consists of one genus and three species living in tropical Africa and India. I believe that the Broscina reached Asia from Gondwanaland, perhaps by way of the Indian subcontinent by the Middle Tertiary time. Therefore, the Broscina may not have played a role in the Ear;y elaphrine evolution. The Melaenini were probably more diverse and might be the closest relative of elaphrines. However, the very limited extant diversity yielded little information except that the elaphroid ancestor might have been tropical. I believe that the common ancestor of the elaphroid (elaphrine and sister group) became widespread and diverse in tropical Asia in the Late Cretaceous but generally became extinct. Only one peripheral ancestor (the immediate elaphrine ancestor) adapted to new niches and survived by invading the restricted temperate area where it diversified and gave rise to ancestors of extant subgenera and genera. I failed to find an explanation for this radiation. This series of events is similar to the hypothesis of taxon cycles presented by Wilson (1961) about ant evolution in Indonesia where peripheral elements adapted to new niches, successfully invaded islands and radiated there. Such patterns have also been described by Darlington (1971) and Ball (1975) for the evolution of high altitude radiation. Whitehead (1976) in his study of the weevil genus Rhinochenus generalises the pattern for any aerially restricted organism potentially affected by climate cycle in braking or expanding its original range (he termed this islandic). In my context the island is the restricted temperate zone where competition is probably less intense.

Species of Diacheila may have been numerous and divergent the Ear;y in the history of the genus, as suggested by the divergent D. polita. Therefore, I suspect that most descendants of the ancestor of Diacheila became extinct as the marsh environment in temperate zones became an area of radiation for more successful competitors (such as Agonum and Bembidion). Only one peripheral ancestor adapted to marshes in subarctic zones survived as this habitat even today shows a very poor diversity of potential competitors. Therefore, a cycle of taxa is the best explanation. Species of Diacheila may have spread in Pliocene times across Beringia, but I suspect their holarctic range was achieved in the Late Pleistocene over Beringia during glacial events.

The history of species of Blethisa is probably similar to the one suggested for species of Diacheila. Basically, I suspect their common ancestor radiated early, but most of its descendants became extinct except for various peripheral elements adapted to unusual marsh habitats where potential competitors (such as Agonum and Bembidion) were few. Most extant species (except B. multipunctata and B. oregona) live in habitats where few other carabids are found. Therefore I propose a taxon cycle where the islands are impoverished marsh habitats. I suspect that surviving ancestors of extant taxa remained close to warm and cold temperate zones. Therefore, exchange in Miocene times was achieved for cold temperate adapted ancestors. I suspect other exchanges occurred in Pliocene and Pleistocene times. E. lapponicus, the sole member of Arctelaphrus, is restricted to very impoverished marsh habitats in subarctic areas. I suspect the past events are similar to those of Diacheila. Briefly members of Arctelaphrus became extinct in milder areas with a surviving ancestor in subarctic moss marshes. I suspect most events occurred in the Siberian center and in the Late Pleistocene the sole extant member spread across the Holarctic region. I assume that E. lapponicus invaded Kodiak Island in the Late Pleistocene and gave rise under the repeated harsh glacial conditions of the refugium to E. lapponicus obliteratus.

The complex past history of the species of Neoelaphrus presented below is summarized in Fig. 172. From the Late Eocene on the temperate zone was enlarging as the climate cooled. Therefore, the ancestor of Neoelaphrus probably spread over wider areas in an evolving warm temperate forest. By the Late Oligocene (30 mybp) the range of this ancestor was over Beringia. But climatic conditions continued to deteriorate and by the Late Miocene (17 mybp), as Alaska was becoming boreal, the ancestral population was divided. The Siberian stock gave rise to the ancestor of the uliginosus group while the North American stock gave rise to the common ancestor of the fuliginosus and cupreus group.

Since no extant species of the uliginosus group are known in North America it is probable that the boreal adaptations shown by E. splendidus are recent and not earlier than the Late Pliocene. The events conducive to evolution of the extant species of this group cannot be interpreted in function of what I know about distribution and geological events of the extant members. I feel that the

E. uliginosus ancestor evolved in Europe and in Pleistocene time extended toward southern France, leaving a subalpine stock that gave rise to E. pyranaeus. E. uliginosus seems to have preadaptation to invade mountains as suggested by the Apennine, Balkan, and Tien-shan mountains populations. Of the extant species, E. splendidus and E. japonicus are least derived. Their relationship to one another is still unknown; however, E. japonicus is still closely associated with mixed mesophytic forests associated with warm temperate climate (the ancestral habitat).

The North American stock gave rise to the extant fuliginosus group that remained closely associated with the mixed mesophytic forest, the ancestral habitat. Present species distributions overlap completely and offer no clues about past events; their niches, though very different, offer no clues; and I failed to find any geological or climatic events that could account for the speciation process of these extant taxa. The amount of divergence achieved suggests that the fuliginosus group evolved quite early in the the Late Miocene or the Early Pliocene and that the speciation process probably occurred somewhere in Canada where the mixed mesophytic forest was widespread.

The North American stock also gave rise to the ancestor of the cupreus group. In time, a successful stock, well-adapted to cold temperate and boreal regions, evolved. This adaptation allowed the common ancestor to spread northward and across Beringia as early as the Late Miocene (17 mybp), or as late as the Middle Pliocene. In Early Pliocene times, between 12 mybp and 10 mybp, Beringia was under the sea (Hopkins, 1967). This event effectively isolated the ancestor of the *cupreus* group into two stocks. The Asiatic stock became the ancestor of the *sibericus* subgroup that gave rise to *E. cupreus* and *E. sibiricus*. The event conducive to this speciation process is unknown, since the extant ranges apparently overlap extensively in Asia. Absence of this subgroup from North America suggests that conditions were too cold from the Middle Pliocene until today for the ancestor to cross. Therefore, the ancestor was only adapted to cold temperate and southern boreal conditions; or it crossed (as suggested by a the Middle Pliocene specimen matching extant *E. sibiricus* from the Canadian Arctic islands), and became extinct in North America in the Late Pliocene after the sea extended over Beringia. The North American stock gave rise to the standing water-adapted *clairvillei* subgroup. This stock also gave rise to the more boreal adapted ancestor of *E. clairvillei* and to the common ancestor of *E. olivaceus* and *E. laevigatus*. The reason for the formation of these two ancestors is unknown. The common ancestor of *E. olivaceus* and *E. laevigatus* was probably very widespread across the continent. However, with development in the Late Pliocene of colder conditions, the ancestral population could have become divided by cold temperate grassland and drier zones in the region of the Great Basin. The stock west of the

Cascades gave rise to *E. laevigatus* and the eastern stock gave rise to *E. olivaceus*.

The relationships among extant members of the subgenus *Elaphrus* is very unsatisfactorily understood. I do not feel confident in retracing their past history. The diversity is greatest in North America especially on the Pacific side and south of 45° N. Structural divergence is also the greatest in this area. In Eurasia, if the very divergent *E. lheritieri* is excluded, then the extant fauna is composed of extremely similar elements. The species of this subgenus occupy all climatic zones where elaphrines are found, but are most diverse in the cold temperate zone. Two species are associated with mixed mesophytic forest (*E. ruscarius*, *E.* species C), and two species are restricted to the warm Mediterranean climate: *E. lheritieri* and *E. viridis*. I also feel that extant Euroasiatic species represent some of the most derived stock and probably evolved from an ancestor related to extant *E. finitimus*. The center of origin of this subgenus is probably in western North America as suggested by the diversity and structural divergence of the fauna. However, the best evidence is presence of the least derived extant member, *E.* species A, which is associated with mountains. Therefore, I think that either in the the Late Oligocene, the common ancestor of this subgenus became associated with mountainous regions and spread successfully along the Rocky Mountain ranges or the group survived in western North America where it radiated. Because of the diversity and degree of structural divergence among Euroasiatic species, I feel that two stocks managed to penetrate into Eurasia by the Late Miocene (17 mybp). During the Pliocene epoch, subarctic stocks in Asia evolved, giving rise to E. tuberculatus, and E. parviceps, species that could have invaded North America by the Late Pleistocene. In North America, the widely overlapping distribution patterns and my lack of understanding of phyletic relationships do not allow me to reconstruct past events. The evolution of this subgenus from a lowland ancestor is difficult to accept, since penetration toward western North America would be retarded until the Late Miocene or the Early Pliocene time. This should have produced a more diverse Eurasian fauna and probably a more diverse fauna in eastern North America. An early diversification during the Oligocene in the Canadian Arctic islands, and perhaps Greenland, would have produced a relatively diversified fauna by the time it was on Beringia. I suspect that the Asiatic fauna would be more divergent than seen today. The extant E. species A, though derived from mountain associated ancestors, could have invaded mountains secondarily from lowland ancestors. Therefore, I feel that the above hypothesis is the best, until relationships are clarified and distribution and classification of Eurasiatic species is better known.

The ancestor of Elaphroterus was probably associated with fast moving waters of mountain origin. Therefore, it invaded this habitat from the Asiatic center of origin when much of the Asiatic ranges were well formed. I suspect that the ancestor of *Elaphroterus* was in Asia, while its sister taxon, the ancestor of subgenus *Elaphrus*, was in Beringia. The least derived species (*E. punctatus* and *E. aureus*) are from the cold temperate zone. From the *E. aureus* ancestor, the ancestor of the *purpurans* group evolved. This ancestor spread over Beringia by the Late Miocene times, but the sea extended again over Beringia, isolating the stock in North America. This stock gave rise to extant *E. purpurans*. The Euroasiatic stock gave rise to *E. ulrichi* and a subarctic species, *E. angusticollis*, that spread widely not earlier than the Late Pliocene. This last species invaded western North America in the Late Pleistocene.

5.3 Conclusion

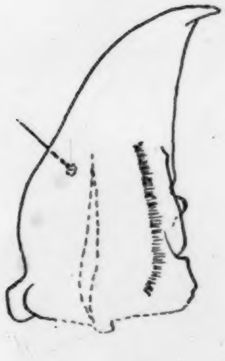
Beringia played a most important role in formation of the flora (Wolfe, 1972) and fauna (Simpson, 1953) of Eurasia and North America. This bridge was in existence during most of the Cenozoic period. The main floral and faunal source areas during the first half of this period was either tropical or temperate Asia (Wolfe, 1972). In the Late Tertiary time North America served also as a source area (Wolfe, 1972, Simpson, 1953). Beringia served mostly as a corridor or filter route for plants and animals adapted to climatic conditions of the bridge. From Paleocene until Oligocene times subtropical and Eocene tropical conditions allowed Asiatic elements to invade North America. Among carabids the following bombardier beetles used this early route: two extant genera of Pheropsophina, and *Neobrachinus* (Erwin , 1970). From the Middle Oligocene until the Late Miocene, numerous temperate Asiatic elements extended into North America. The exchange was extensive as today extant genera and subgenera are shared. In carabids the following genera used this route then: *Loricera* (Ball and Erwin, 1969), *Badister* (Ball, 1959), *Diplocheila* (Ball, 1959), *Dicaelus* (Ball, 1959), and *Dicheirus* (Noonan, 1975). In Pliocene times boreal elements from both continents are exchanged. These elements are mostly derived from temperate elements on each continent. Finally Beringia is the seat of exchange of subarctic and arctic elements in the Late Pleistocene during some of the glacial periods as suggested by numerous holarctic species of plants and animals shared today (Hultén, 1968 and Lindroth, 1961 to 1969, Ball, 1966), and confirmed by unchanged glacial fossils observed by Lindroth (1969), Coope, (1970) and Matthews (1970, 1974a and 1974b). However, speciation may have occurred during the Pleistocene for subtropical or tropical animals with limited dispersal powers as suggested by Whitehead (1976) and Howden (1963, 1966, 1969).

In summary, ancestral and extant members of *Elaphrus* crossed Beringia several times starting with one Euroasiatic wave from the postulated Siberian center of origin to North America and Eurasia. The sole member of *Arctelaphrus* invaded

North America during one of the glacial periods in the Late Pleistocene. In Neoelaphrus one early invasion from Asia occurred in the Late Oligocene followed by another in the Late Miocene from North America. In Elaphrus one invasion to Eurasia was made by one or two elements followed by invasion of North America by two of their descendants during a glacial period in the Late Pleistocene. In Elaphroterus one stock invaded North America in the Late Miocene followed by another one during one of the glacial periods of the the Late Pleistocene.

The history of elaphrines is similar to many elements of the temperate biota. In the Late Cretaceous the temperate biome is derived from various marginal elements from the tropics. This process continues during the first half of the Tertiary period as the temperate zone enlarged due to climatic deterioration. The history of many ancestors of extant taxa in the temperate zone is similar to Wilson's (1961) ant study in the Oriental Melanesian region, also similar to studies by Darlington (1971) and Ball (1975) of high altitude biota. Wilson termed the zoogeographic event: "taxon cycle". Basically, expanding taxa are from large and old land masses where competition is intensive. These taxa have species adapted to marginal habitats. If one of these reaches an area of low diversity and competition pressure it tends to occupy successfully unused habitats and even to dislodge species with overlapping habitats. These species become "ecologically released" as competition pressure is lowered. Therefore, the descendants of these taxa are not likely to successfully invade areas of intense competition where their ancestors came from. Therefore, these species are more likely to evolve in the area of origin or to invade smaller land masses or land masses with very immature faunas. Therefore, the taxon can maintain itself, expanding and contracting, or become extinct in the area, or shift to smaller land masses. Wilson, in his work, spoke of islands. I feel islands should be considered in more general terms including areas with immature fauna and flora. For example, the the Late Cretaceous temperate zone was small and relatively recent, or today _Sphagnum_ bogs are islands of impoversihed fauna. The same can be said of the Miocene boreal zone, or of the Late Pliocene arctic zone. Therefore, an expanding taxon may have marginal elements adapting to these zones and even radiating in them. But as this zone enlarges and becomes older the diversity and also competition pressure increase leaving taxa able to survive the pressure but replacing those unable to. Thus marginal elements are potentially able to invade new zones of low competition pressure and be the only surviving element of a taxon. I feel this happened not only with the elaphrine ancestor, or the ancestors of extant _Diacheila_, _Blethisa_ and _Arctelaphrus_ but during the evolution of the mixed mesophytic forest (Wolfe, 1972). Among carabids studied, _Dicaelus_ (Ball, 1959), _Loricera_ (Ball and Erwin, 1969) probably followed a similar pattern. In conclusion, I feel that the origin of the elaphrines, the mixed mesophytic forest, or for that matter, the origin of temperate, boreal and arctic biota can be best explained by the principle of taxon cycles as outlined above.

Fig. 1-8. Illustration of structures of adult Elaphrini. Fig. 1-4. Mandible. 1. Mandible of *B*. *quadricollis* Haldeman, ventral aspect, a) right, b) left. 2. Right mandible of *D*. *polita* Faldermann, ventral aspect. 3. Right mandible of *E*. *lapponicus* Gyllenhal, a) ventral aspect, b) internal aspect. 4. Right mandible of *E*. *parviceps* Van Dyke, ventral aspect. Fig. 5-7. Maxilla, ventral aspect. 5. *D*. *polita* Faldermann. 6. *B*. *quadricollis* Haldeman. 7. *E*. *lapponicus* Gyllenhal. 8. Gula and labium of *D*. *polita* Faldermann, ventral aspect.



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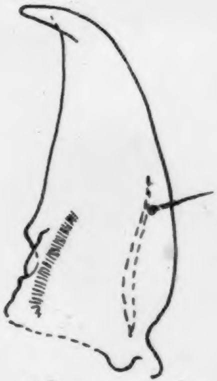

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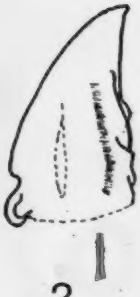

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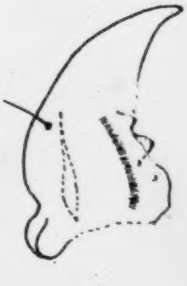

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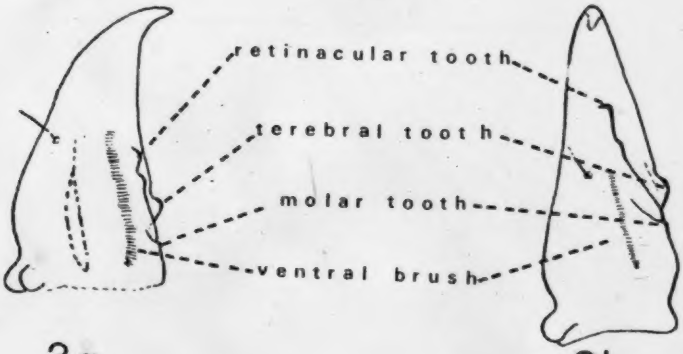

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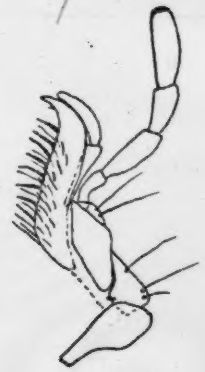

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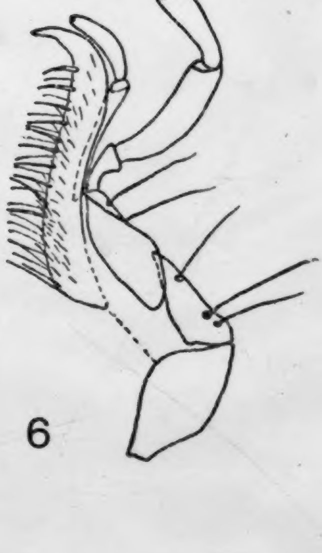

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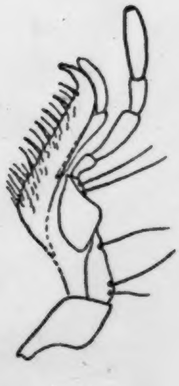

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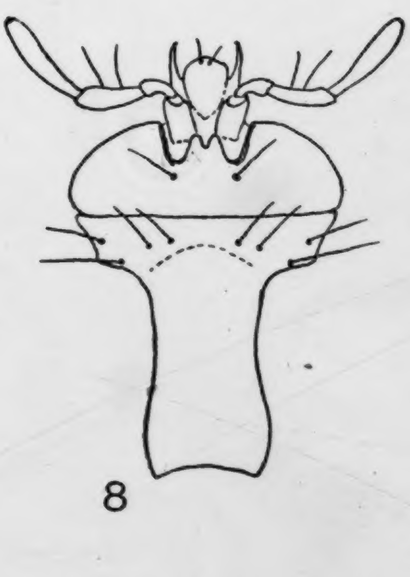

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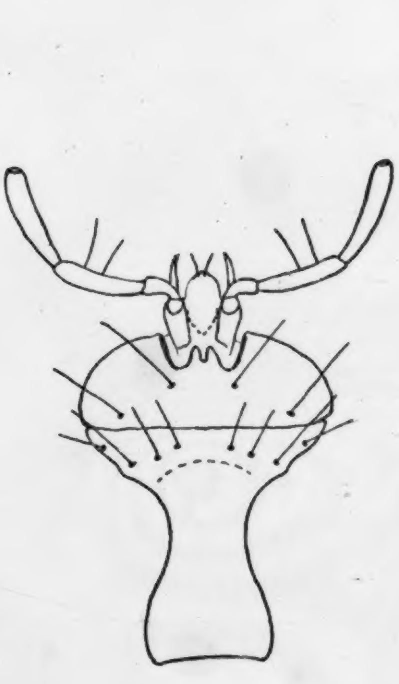
Fig. 9-17. Illustration of structures of adult Elaphrini. Fig. 9-10. Gula and labium, ventral aspect. 9. B. quadricollis Haldeman. 10. E. lapponicus Gyllenhal. Fig. 11-13. Antennomeres 1-4, dorsal aspect. 11. E. riparius Linnaeus, Skane, Sweden. 12. E. parviceps Van Dyke, Anderson River delta, Northwest Territories. 13. E. lecontei Crotch, Spring Creek Basin, Alberta. Fig. 14-16. Head, dorsal aspect. 14. D. polita Faldermann. 15. B. multipunctata Linnaeus. 16. E. lapponicus Gyllenhal. 17. Pronotum of E. uliginosus Fabricius, a) dorsal aspect, b) lateral aspect.



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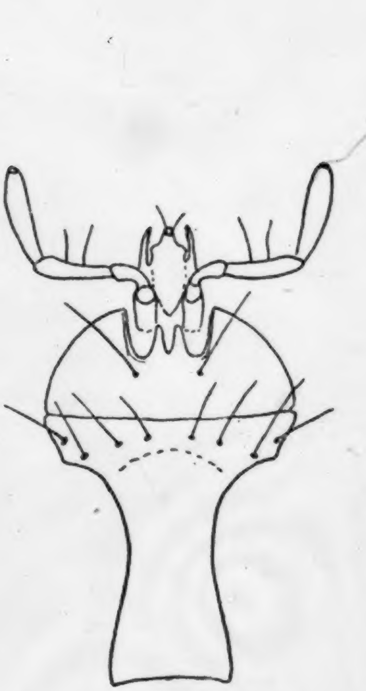

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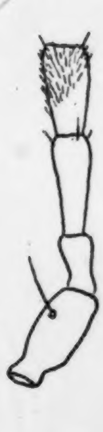

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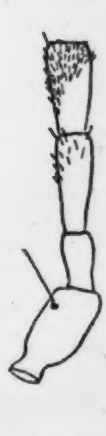

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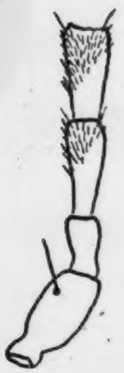

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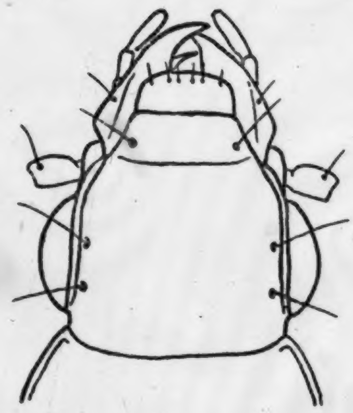

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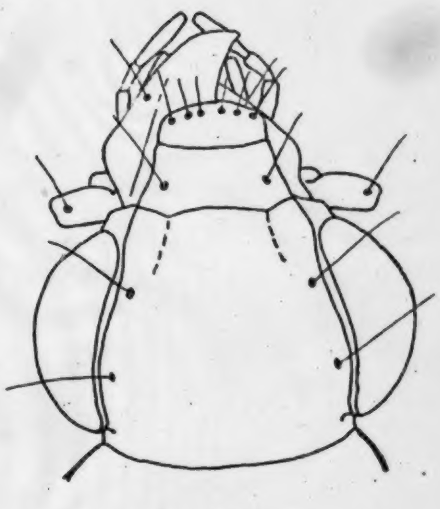

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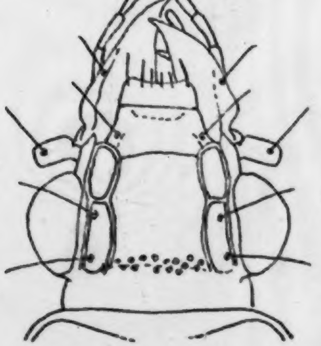

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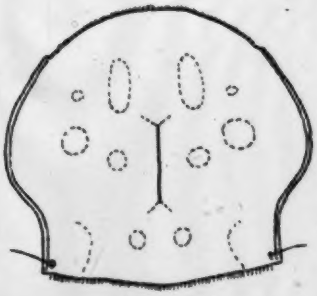

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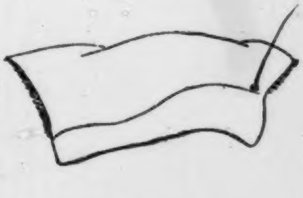

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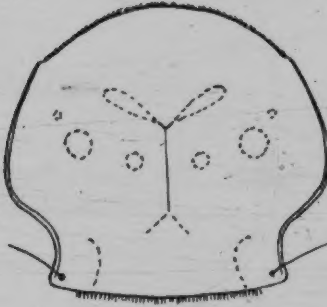
Fig. 18-31. Illustration of structures of adult Elaphrini. Fig. 18. Pronotum of *E. fuliginosus* Say, a) dorsal aspect, b) lateral aspect. Fig. 19-25. Pronotum, dorsal aspect. 19. *E. cupreus* Duftschmid, Skane, Sweden. 20. *E.* species A, Pullman, Washington. 21. *E.* species B, Anguin, California. 22. *E. viridis* Horn, 7 mi. s. Dixon, California. 23. *E. lheritieri* Antoine, Safi, Morroco. 24. *E. lecontei* Crotch, Pakowski Lake, Alberta, 25. *E. riparius* Linnaeus, Skane, Sweden. Fig. 26-27. Pronotum, lateral aspect. 26. *E. angusticollis angusticollis* Sahlberg, Aklavik, Northwest Territories. 27. *E. purpurans* Hausen, McMinnville, Oregon. Fig. 28-31. Elytral striae 2 (right) and 3 (left), discal portion. 28. *D. polita* Faldermann. 29. *B. eschscholtzi* Zoubkoff. 30. *B. quadricollis* Haldeman. 31. *E. lapponicus* Gyllenahl.



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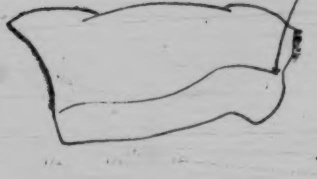

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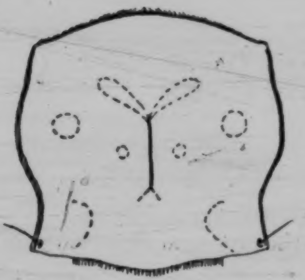

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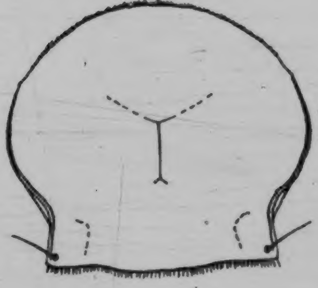

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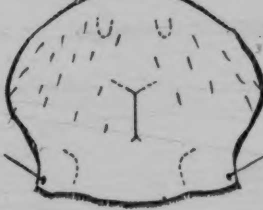

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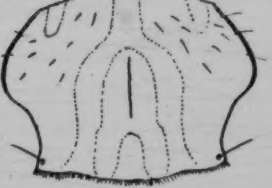

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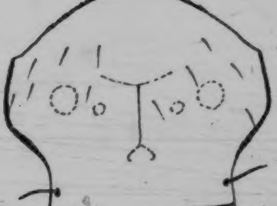

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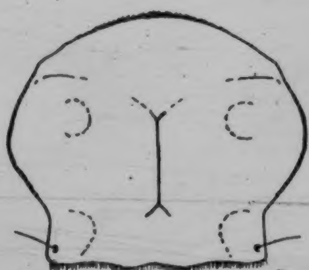

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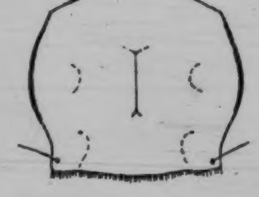

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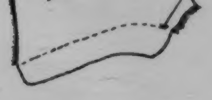

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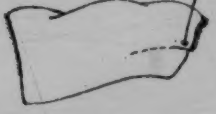

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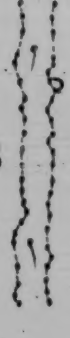

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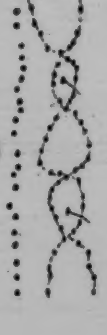

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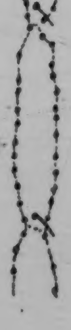

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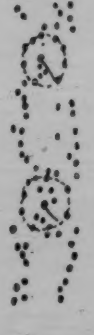
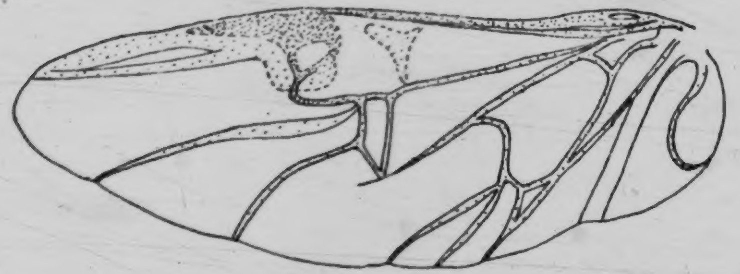


Fig. 32-38. Illustration of structures of adult Elaphrini. Fig. 32-33. Hindwing. 32. E. americanus Dejean. 33. Oblongum of B. multipunctata Linnaeus. Fig. 34-35. Apico-posterior surface of hind femur. 34. E. americanus Dejean, George Lake, Alberta. 35. E. californicus Mannerheim, Dayton, Alberta. Fig. 36. Male genitalia of Broscus cephalotes (redrawn from Ball, 1956), a) median lobe lateral aspect, b) detail of internal sac (inverted) showing sclerites X and Y, lateral view, c) left paramere, d) right paramere. Fig. 37-38. Male genitalia, a) lateral aspect of median lobe and internal sac, c) left paramere, d) right paramere. 37. Melaenius piger. 38. D. arctica Gyllenhal.



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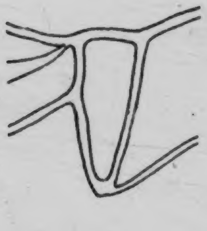

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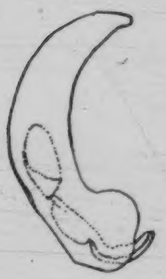

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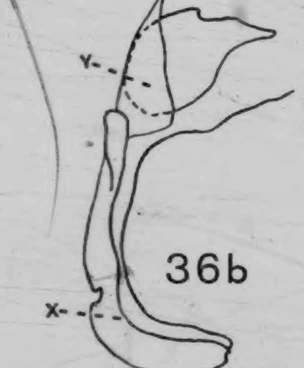

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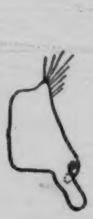

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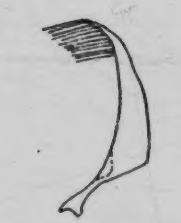

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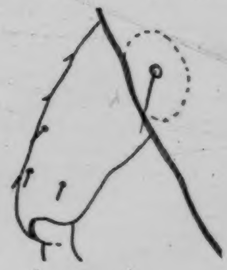

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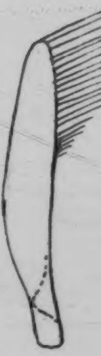

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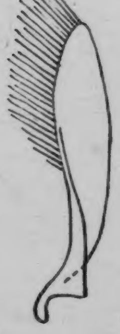

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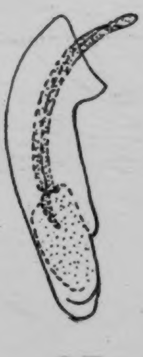

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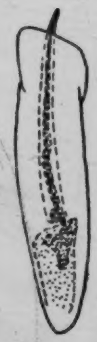

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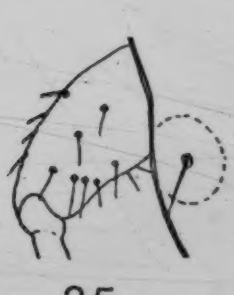

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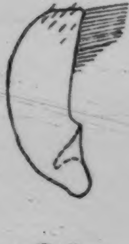

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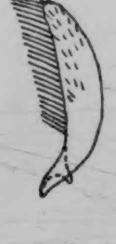

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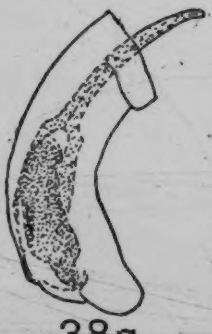

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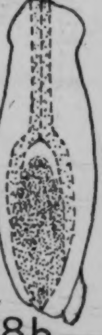
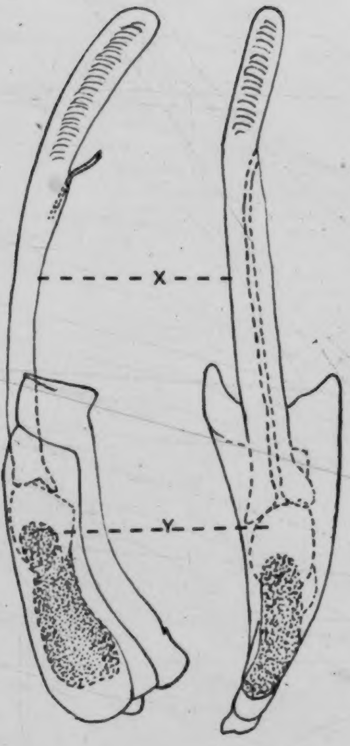


38b

Fig. 39-45. Illustration of structures of adult Elaphrini. Fig. 39-45. Male genitalia (black vertical line = 100 microns). Fig. 39-40. Male genitalia a) lateral aspect of median lobe and internal sac, b) dorsal aspect of median lobe and internal sac, c) left paramere, d) right paramere. 39. B. multipunctata Linnaeus. 40. E. lapponicus obliteratus Mannerheim, Kodiak Island, Alaska. Fig. 41. Male genitalia of E. splendidus Fischer von Waldheim, Omsuktschan, USSR, a) apex of median lobe, dorsal aspect, b) apex of median lobe, lateral aspect, c) left paramere, d) right paramere. Fig. 42-45. Male genitalia, apex of median lobe, a) dorsal aspect, b) lateral aspect. 42. E. japonicus Ueno, Amoari Pref., Japan. 43. E. uliginosus Fabricius, Skane, Sweden. 44. E. pyrenaeus Fairmaire and Laboulbène, Lago Llebreta, Bohi, Spain. 45. E. fuliginosus Say, Illinois.



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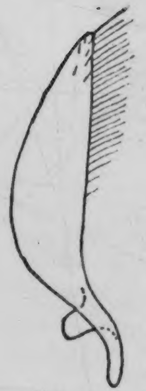

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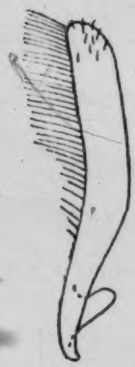

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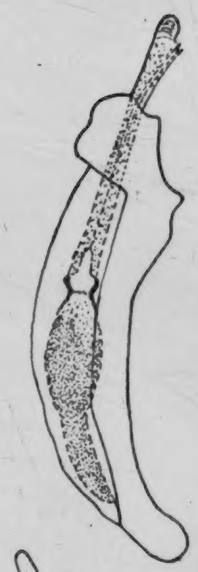

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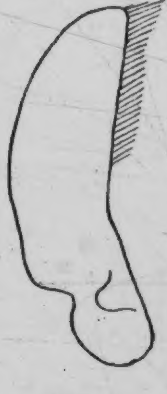

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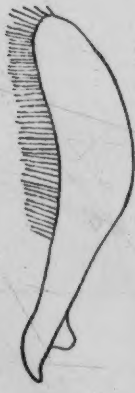

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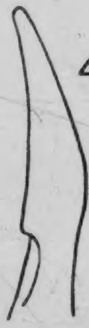

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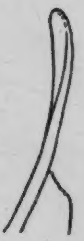

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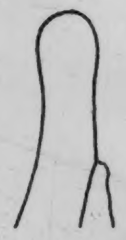

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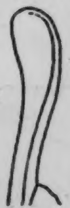

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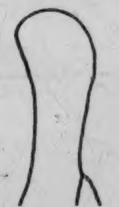

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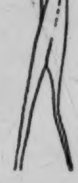

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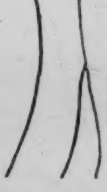

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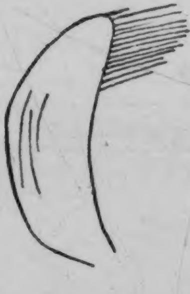

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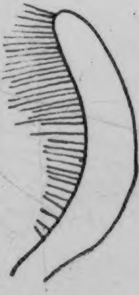

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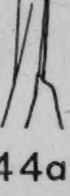

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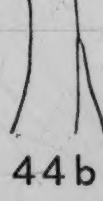

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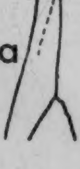

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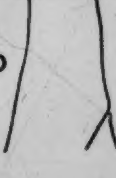
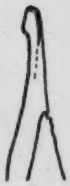


45b

Fig. 46-56. Illustration of structures of adult Elaphrini. Fig. 46-56. Male genitalia (black vertical line = 100 microns). Fig. 46-52. Male genitalia, apex of median lobe, a) dorsal aspect, b) lateral aspect. 46. *E. lindrothi* new species, Maryland, Bowie. 47. *E. cicatricosus* LeConte, Maclean Bog, New York. 48. *E. sibiricus* Motschulsky, Rebun Island, Hokkaido, Japan. 49. *E. cupreus* Duftschmid, Skane, Sweden. 50. *E. clairvillei* Kirby, Ministik Lake, Alberta. 51. *E. olivaceus* LeConte, Meach Lake, Quebec. 52. *E. laevigatus* LeConte, San Francisco, California. Fig. 53. Male genitalia of *E. punctatus* (Ibaragi Pref., Japan, a) lateral aspect of median lobe, b) left paramere, c) right paramere. Fig. 54. Male genitalia, apex of median lobe of *E. punctatus* Motschulsky, Irkutsk, USSR, a) ventral aspect, b) lateral aspect. Fig. 55. Male genitalia, median lobe of *E. aureus* Müller, Pont St.-Esprit, France, a) lateral aspect, b) ventral aspect of apex, c) lateral aspect of apex. Fig. 56. Male genitalia of *E. purpurans* Hausen, McMinnville, Oregon, a) lateral aspect of median lobe, b) right paramere, c) ventral aspect of apex of median lobe.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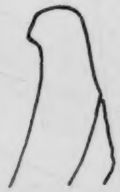
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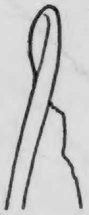
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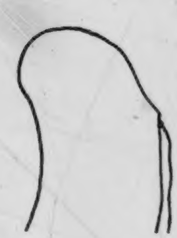
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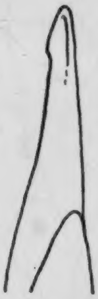
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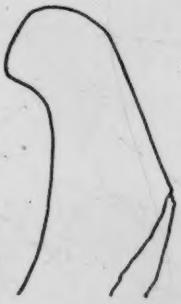
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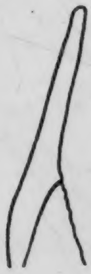
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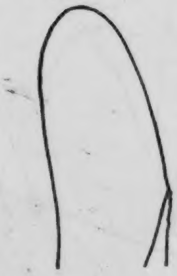
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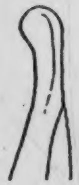
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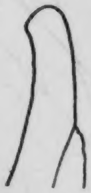
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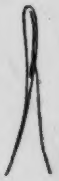
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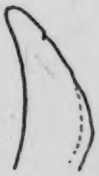
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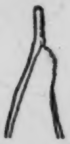
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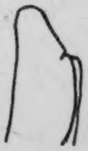
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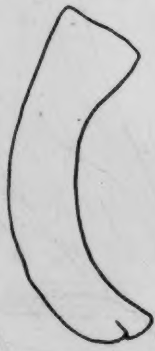
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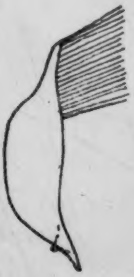
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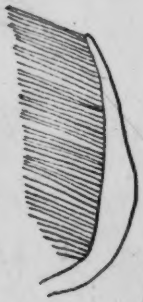
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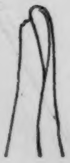
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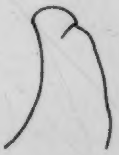
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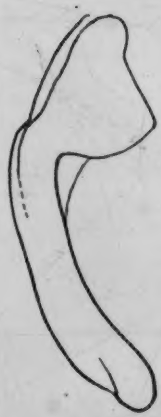
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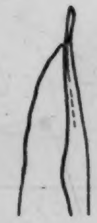
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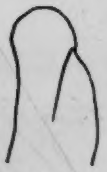
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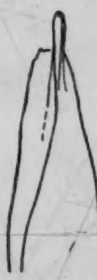
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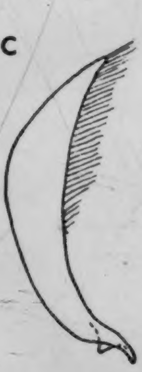
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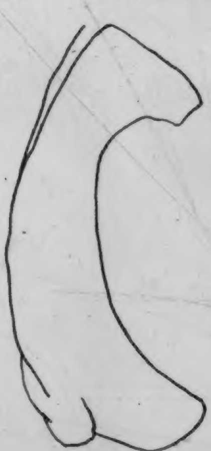
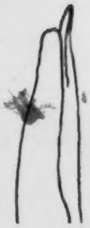

56a

Fig. 57-69. Illustration of structures of adult Elaphrini. Fig. 57-69. Male genitalia (black vertical line = 100 microns). Fig. 57. Apex of median lobe of *E. angusticollis jakowlewi* Semenov, Metsapirti, USSR, a) ventral aspect, b) lateral aspect. Fig. 58. Apex of median lobe of *E. angusticollis angusticollis* Sahlberg, Omsukschan, USSR, lateral aspect. Fig. 59. Apex of median lobe of *E. ulrichi* Redtenbacher, Wien, Austria, a) ventral aspect, b) lateral aspect. Fig. 60-61. Median lobe, a) lateral aspect, b) ventral aspect of apex. 60. *E. ruscarius* Say, Houston Co., Texas. 61. *E. riparius* Linnaeus, Skane, Sweden. 62. Male genitalia of *E. hypocrita* Semenov, Wernyi, USSR, a) lateral aspect of apex of median lobe, b) right paramere. Fig. 63-68. Apex of median lobe, a) ventral aspect, b) lateral aspect. 63. *E.* species C, Harbin, China. 64. *E. lheritieri* Antoine, Safi, Morocco. 65. *E. lecontei* Crotch, Pakowski Lake, Alberta. 66. *E. finitimus* Casey, Tocaloma, California. 67. *E. americanus* Dejean, Pullman, Washington. 68. *E. americanus* Dejean, Seattle, Washington. 68. *E. americanus* Dejean, Seattle, Washington. Fig. 69. Male genitalia of *E. americanus* Dejean, Spring Creek Basin, Alberta, a) ventral aspect of median lobe, b) lateral aspect of median lobe, c) right paramere.



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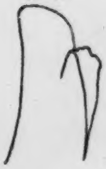

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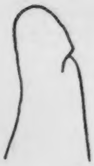

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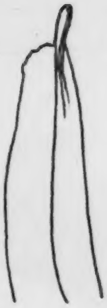

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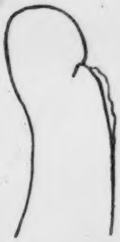

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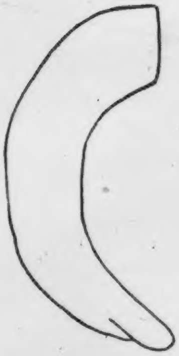

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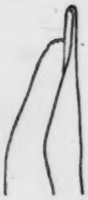

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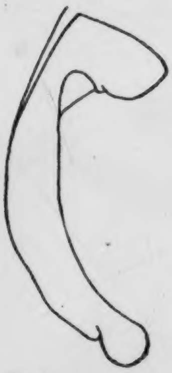

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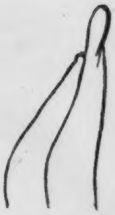

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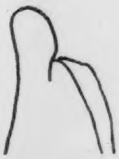

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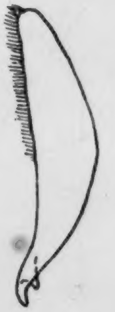

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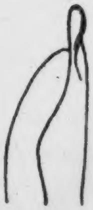

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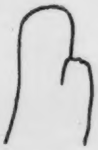

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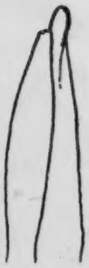

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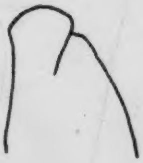

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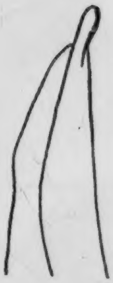

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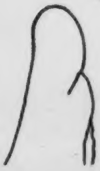

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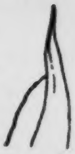

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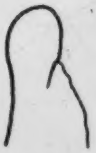

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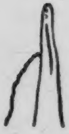

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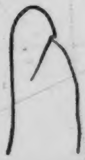

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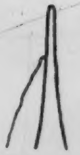

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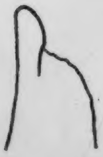

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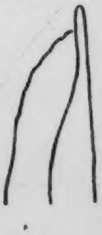

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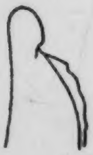

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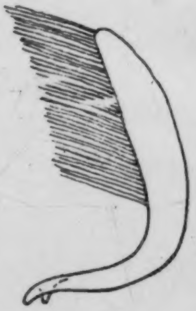
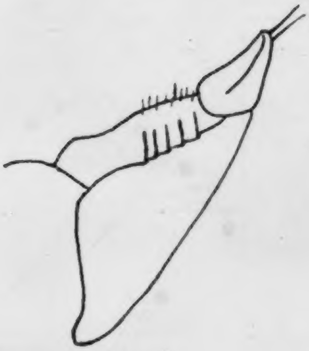


69c

Fig. 70-75. Illustration of structures of adult Elaphrini. Fig. 70-75. Stylus of ovipositor, lateral aspect. 70. *D. polita* Faldermann. 71. *B. multipunctata* Linnaeus. 72. *E. lapponicus obliteratus* Mannerheim. 73. *E. clairvillei* Kirby. 74. *E. purpurans* Hausen. 75. *E. lecontei* Crotch. Fig. 76. Code for setae and pores of first instar larva of *E. clairvillei* Kirby, a) dorsal aspect of the head, b) ventral aspect of the head.



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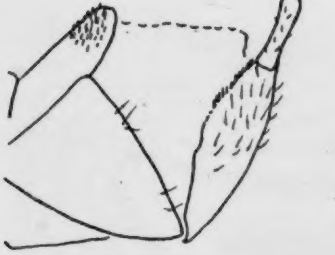

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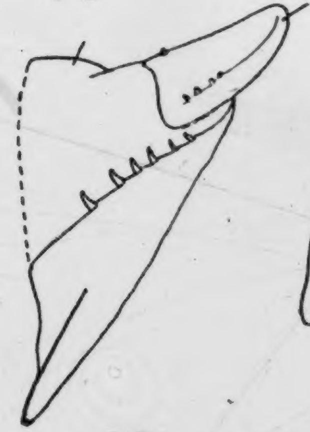

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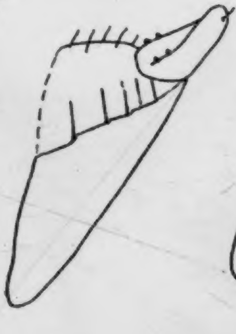

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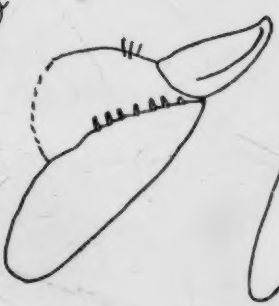

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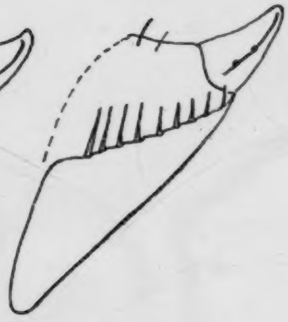

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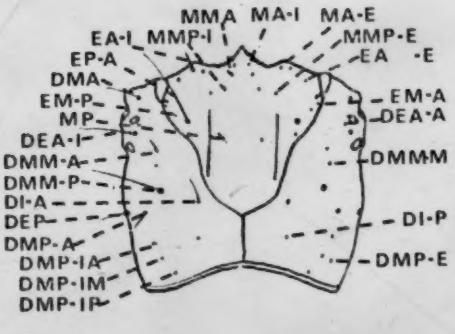

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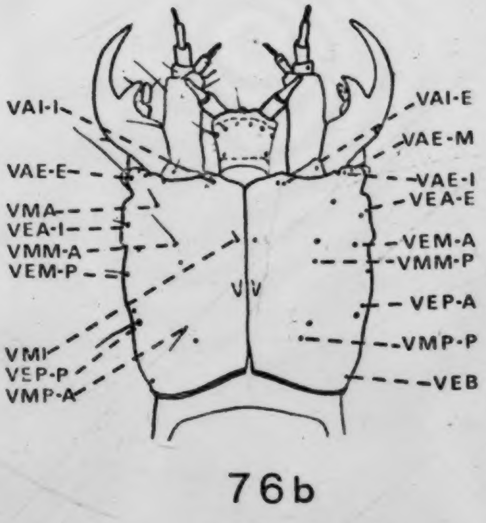
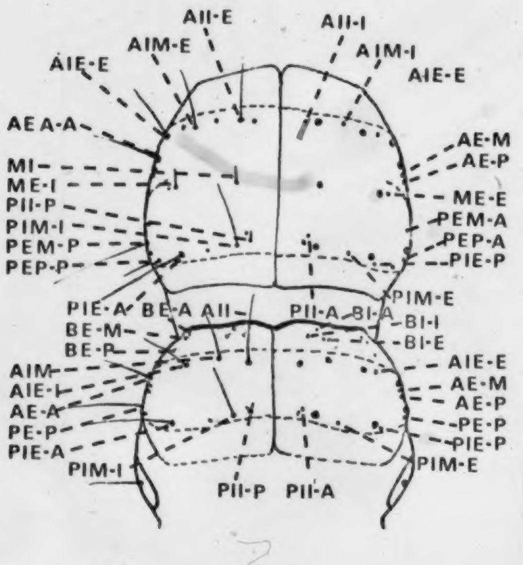


76b

Fig. 76. Code for setae and pores of first instar larva of E. *clairvillei* Kirby, c) dorsal aspect of prothorax and mesothorax, d) ventral aspect of prothorax and mesothorax, e) dorsal aspect of abdominal segments 8, 9, and 10, f) ventral aspect of abdominal segments 7, 8 and 9, g) lateral aspect of abdominal segments 9 and 10.



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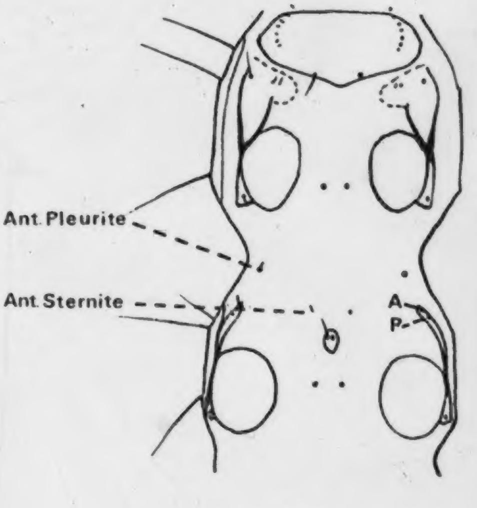

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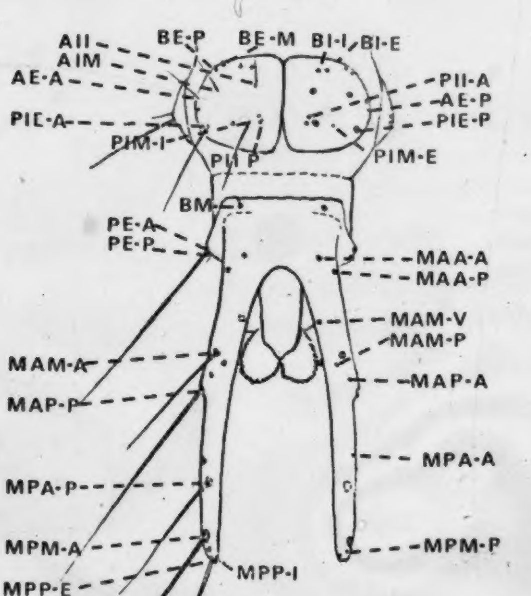

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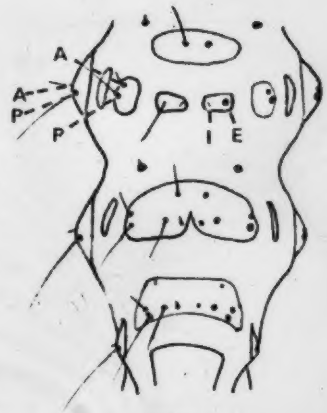

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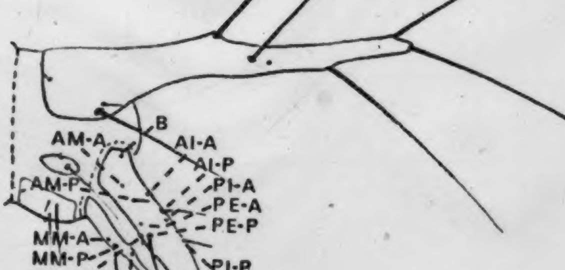
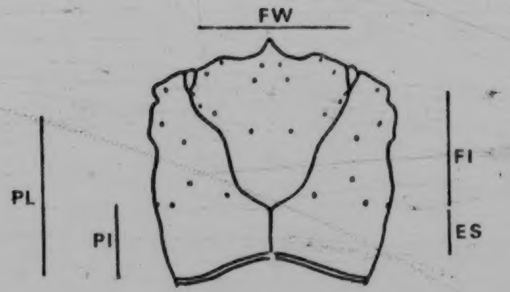


76g

Fig. 77-83. Illustration of structures of larval Elaphrini. Fig. 77. Measurements and their code of first instar larva of E. clairvillei Kirby, a) dorsal aspect of head capsule, b) ventral aspect of head capsule. Fig. 78-81. Mandible. 78. Third instar larva of D. arctica Gyllenhal (redrawn from Lindroth, 1954). 79. First instar larva of D. polita Faldermann. 80. First instar larva of E. clairvillei Kirby. 81. First instar larva of E. lecontei Crotch. Fig. 82. Labium of first instar larva of E. clairvillei Kirby, a) dorsal aspect, b) ventral aspect. Fig. 83. Maxilla of D. polita Faldermann, a) dorsal aspect, b) ventral aspect, c) lacinia.



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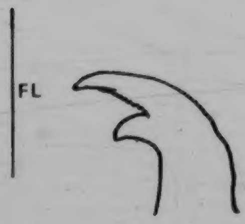

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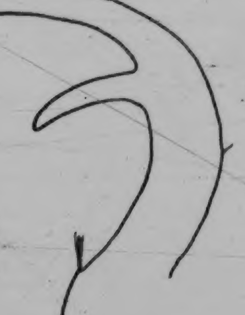

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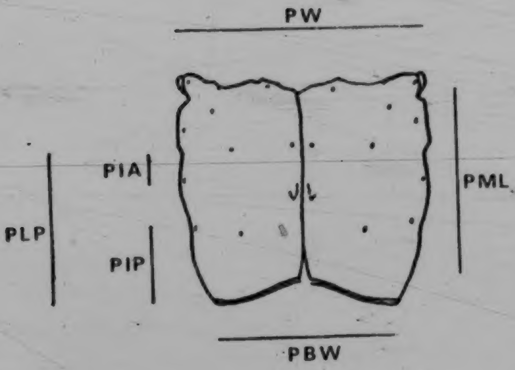

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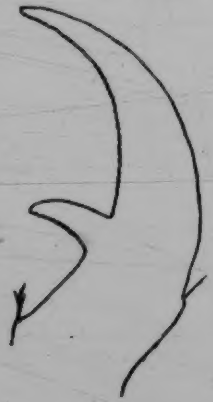

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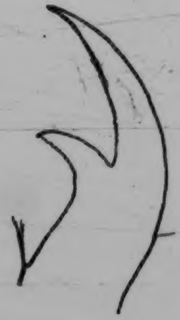

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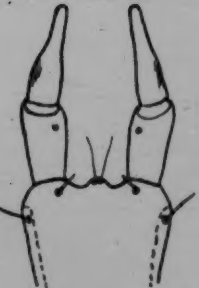

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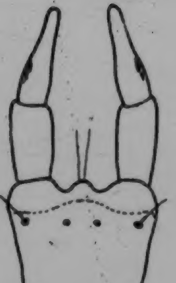

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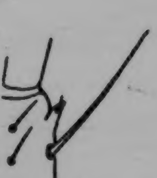

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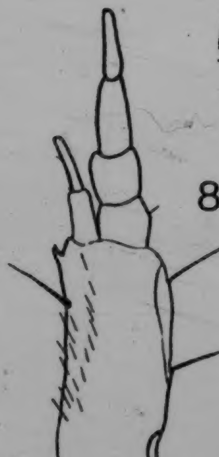

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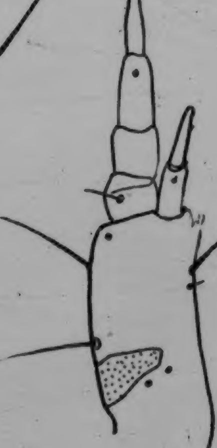
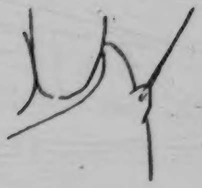


83b

Fig. 84-89. Illustration of structures of larval Elaphrini. Fig. 84. Lacinia of *D. arctica* Gyllenhal (redrawn from Lindroth, 1954). Fig. 85. Maxilla of *E. clairvillei* Kirby, a) dorsal aspect, b) ventral aspect, c) lacinia. Fig. 86. Lacinia of *E. purpurans* Hausen. Fig. 87-89. Head, a) dorsal aspect, b) nasale. 87. *D. polita* Faldermann. 88. *B. quadricollis* Haldeman. 89. *E. lapponicus lapponicus* Gyllenhal.



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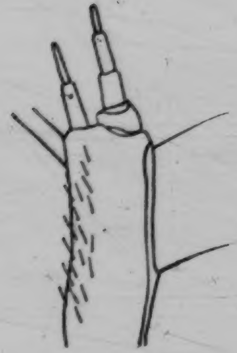

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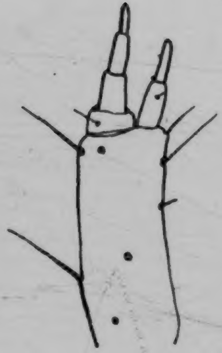

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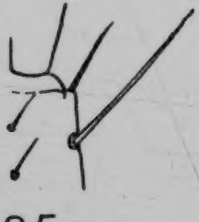

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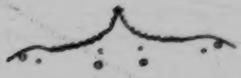

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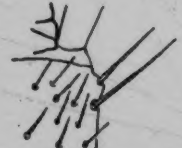

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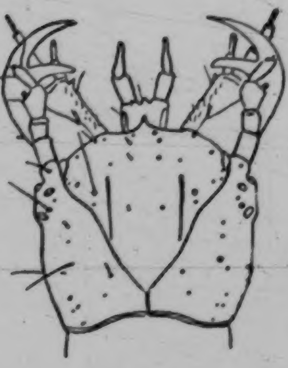

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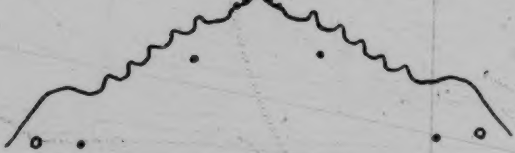

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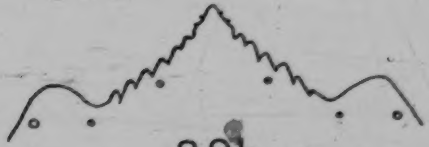

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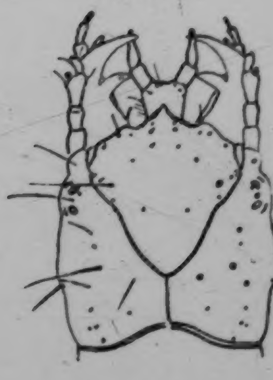

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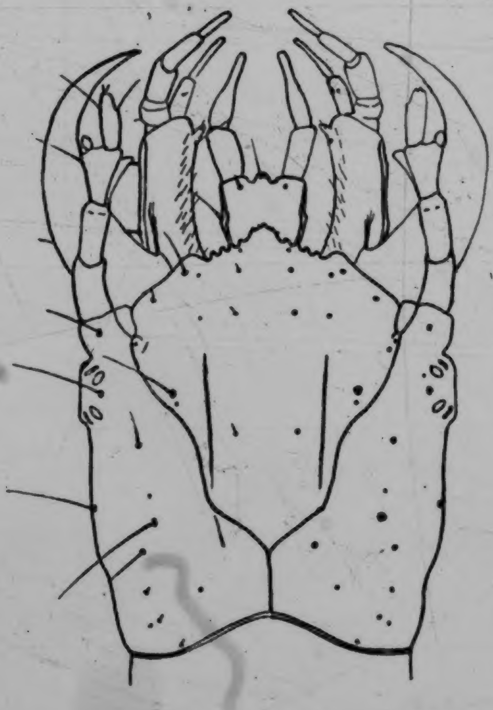
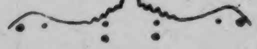


88a

Fig. 90-97. Illustration of structures of larval Elaphrini. Fig. 90-92. Head, a) dorsal aspect, b) nasale. 90. *E. clairvillei* Kirby. 91. *E. lecontei* Crotch. 92. *E. purpurans* Hausen. Fig. 93-97. Abdominal tergum 9, lateral aspect. 93. *D. polita* Faldermann, a) first, b) second instar larva. 94. *D. arctica* Gyllenhal, third instar larva. 95. *B. quadricollis* Haldeman, first instar larva. 96. *B. multipunctata* Linnaeus, a) second, b) third instar larva. 97. *E. lapponicus lapponicus* Gyllenhal, third instar larva.



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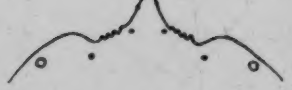

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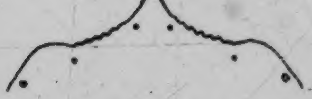

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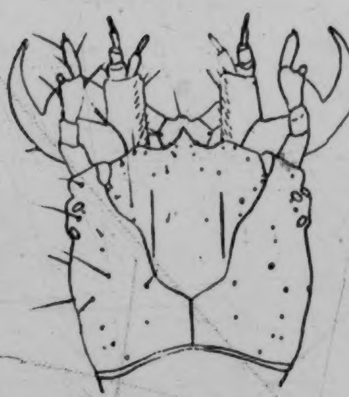

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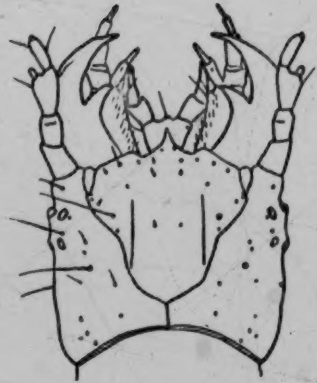

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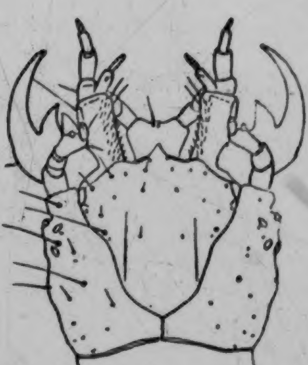

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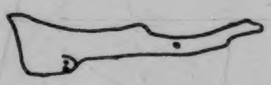

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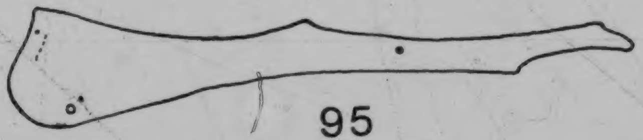

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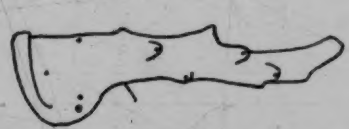

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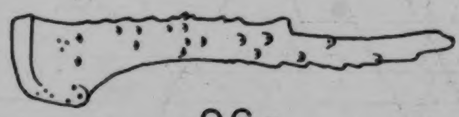

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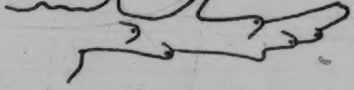

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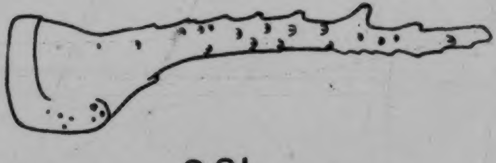

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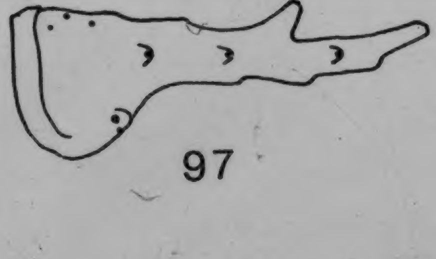

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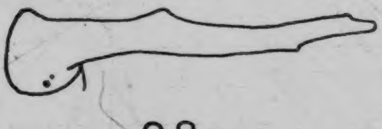
Fig. 98-103. Illustration of structures of larval Elaphrini. Abdominal tergum 9, lateral aspect. 98. *E. clairvillei* Kirby, a) first, b) second, c) third instar larva. 99. *E. cicatricosus* LeConte, a) second, b) third instar larva. 100. *E. americanus* Dejean, a) second, b) third instar larva. 101. *E. aureus* Müller, a) second, b) third instar larva. 102. *E. purpurans* Hausen, third instar larva, a) McMinnville, Oregon, b) Conjuring Creek, Alberta. 103. *E. ulrichi* Redtenbacher, a) second, b) third instar larva.



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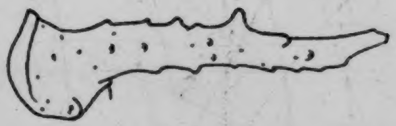

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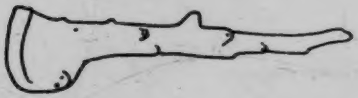

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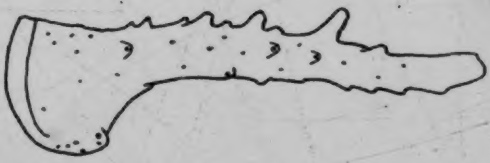

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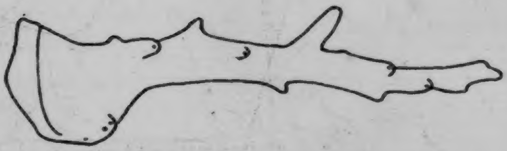

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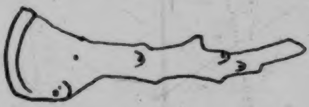

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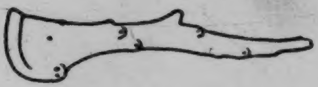

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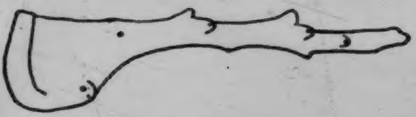

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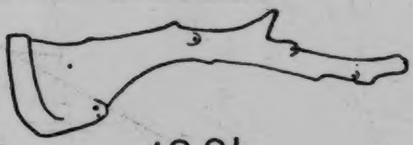

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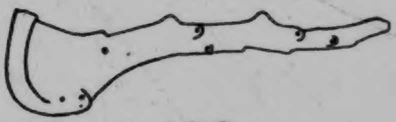

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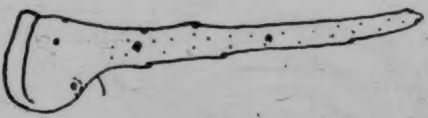

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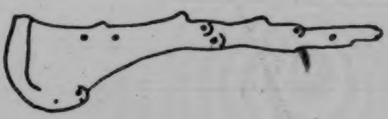

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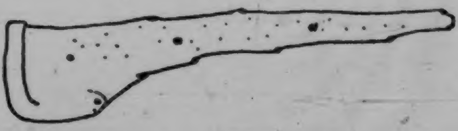
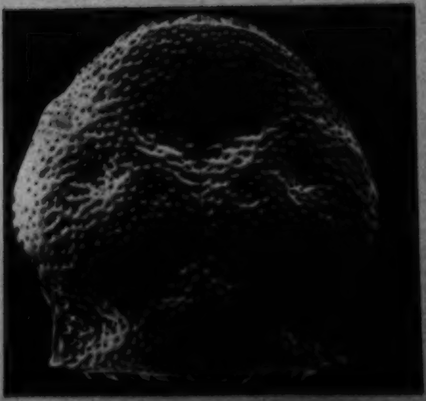


103b

Fig. 104-109. Scanning electron micrographs of strucutres of adult Elaphrini. Fig. 104-106. Pronotum, dorsal aspect. 104. *E. lindrothi* new species, Bowie, Maryland. 105. *E. lheritieri* Antoine, Safi, Morocco. 106. *E. viridis* Horn, California. Fig. 107-109. Pronotum and prosternum, lateral aspect. 107. *E. cicatricosus* LeConte, Maclean Bog, New York. 108. *E. cupreus* Duftschmid, Skane, Sweden. 109. *E. ruscarius* Say.



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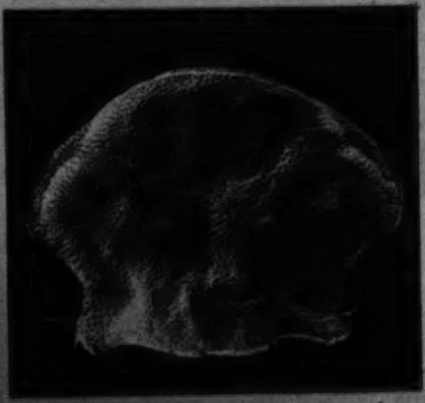

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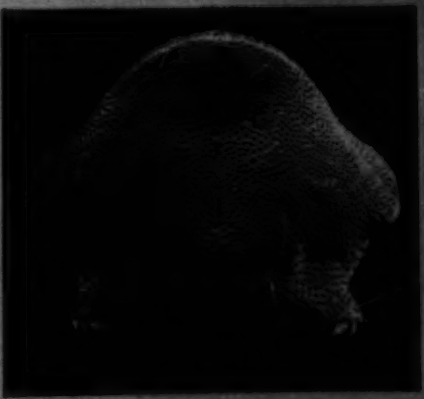

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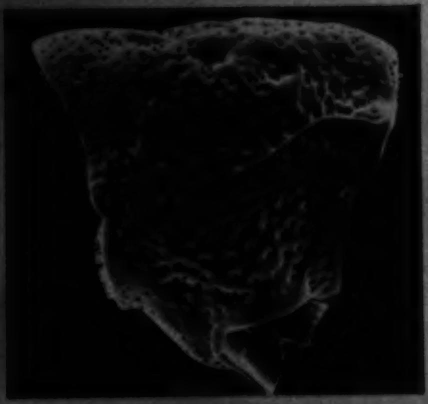

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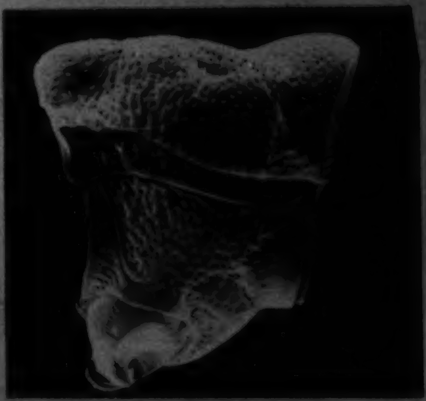

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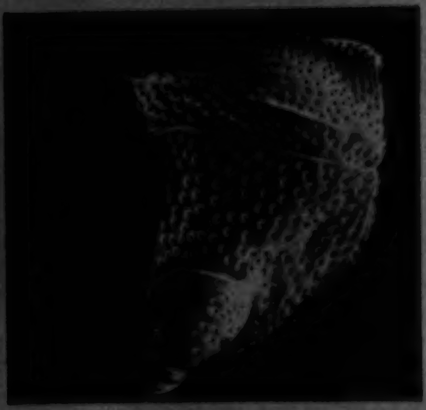

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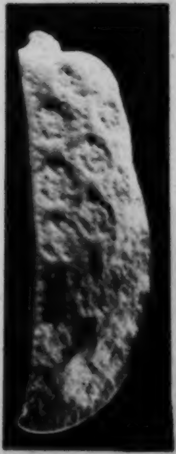
Fig. 110-121. Scanning electron micrographs of strucutres of adult Elaphrini. Fig. 110-117. Elytron. 110. *E. lapponicus lapponicus* Gyllenhal, Dawson, Yukon. 111. *E. clairvillei* Kirby, George Lake, Alberta. 112. *E. punctatus* Motschulsky, Japan. 113. *E. angusticollis angusticollis* Sahlberg, Aklavik, Northwest Territories. 114. *E. viridis* Horn, California. 115. *E. lheritieri* Antoine, Safi, Morocco. 116. *E. parviceps* Van Dyke, Coppermine, Northwest Territories. 117. *E. americanus* Dejean, George Lake, Alberta. Fig. 118-121. Elytral pits on interval 3 (right) and 5, discal portion. 118. *E. lapponicus obliteratus* Mannerheim, Kodiak Island, Alaska. 119. *E. uliginosus* Fabricius, Skane, Sweden. 120. *E. pyrenaeus* Fairmaire amd Laboulbène, Pyrenee. 121. *E. lindrothi* new species, Bowie, Maryland.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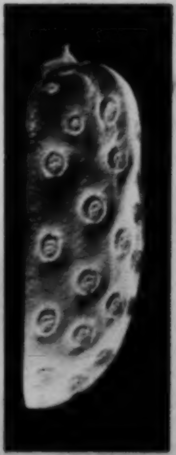
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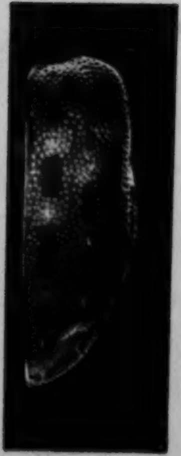
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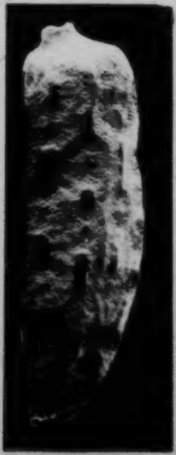
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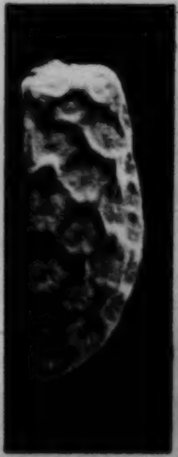
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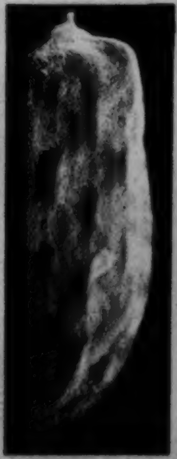
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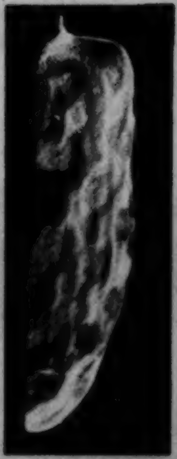
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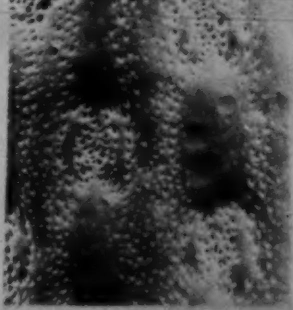
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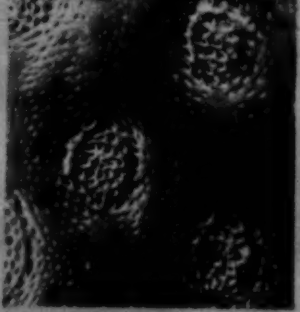
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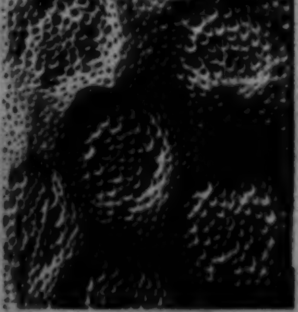
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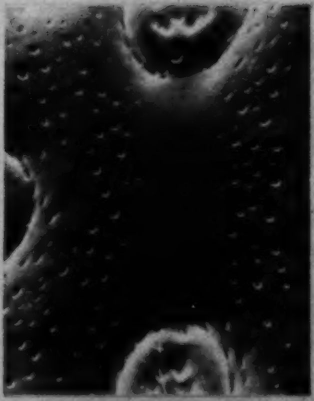
Fig. 122-130. Scanning electron micrographs of strucutres of adult Elaphrini. Fig. 122-130. Elytral pits on interval 3 (right) and 5, discal portion. 122. *E. clairvillei* Kirby, George Lake, Alberta. 123. *E. olivaceus* LeConte, George Lake, Alberta. 124. *E. punctatus* Motschulsky, Japan. 125. *E. angusticollis angusticollis* Sahlberg, Aklavik, Northwest Territories. 126. *E. viridis* Horn, California. 127. *E. lheritieri* Antoine, Safi, Morocco. 128. *E. americanus* Dejean, George Lake, Alberta. 129. *E. parviceps* Van Dyke, Coppermine, Northwest Territoties. 130. *E. lecontei* Crotch, Pakowski Lake, Alberta.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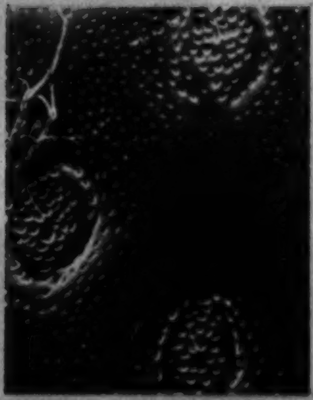
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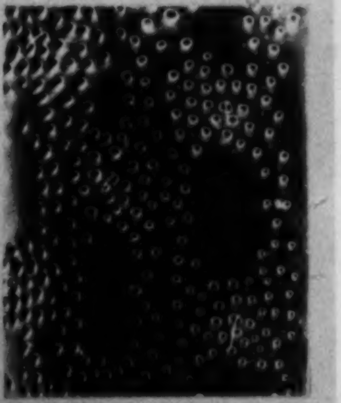
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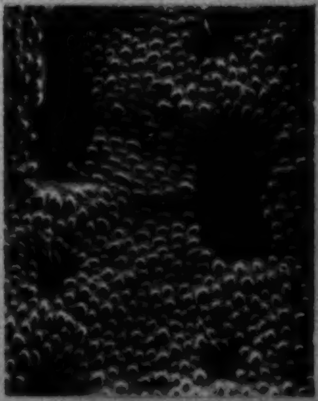
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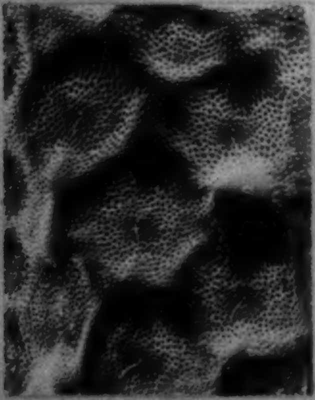
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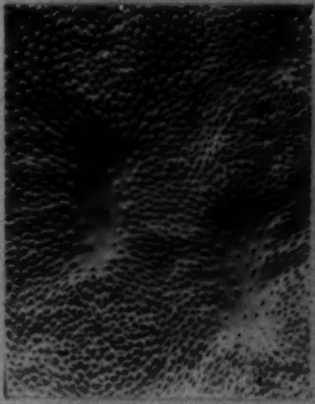
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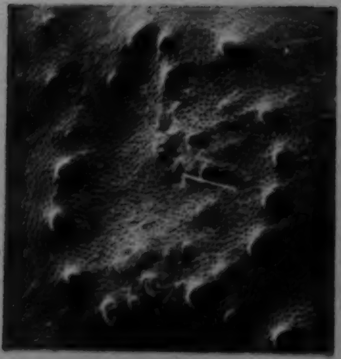
Fig. 131-138. Scanning electron micrographs of strucutres of adult Elaphrini. Fig. 131-136. First sutural pit of elytron. 131. *E. lapponicus obliteratus* Mannerheim, Kodiak Island, Alaska. 132. *E. cupreus* Duftschmid, Skane, Sweden. 133. *E. clairvillei* Kirby, George Lake, Alberta. 134. *E. olivaceus* LeConte, George Lake, Alberta. 135. *E. americanus* Dejean, George Lake, Alberta. 136. *E. parviceps* Van Dyke, Coppermine, Northwest Territories. Fig. 137-138. Microsculpture development on elytral interval 4. 137. *E. uliginosus* Fabricius, Skane, Sweden. 138. *E. pyrenaeus* Fairmaire and Laboulbene, Pyrenee.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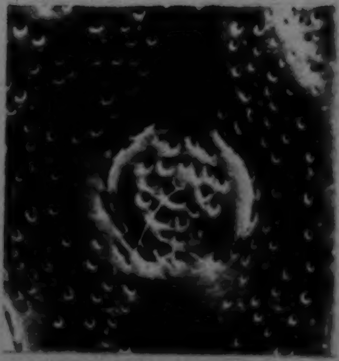
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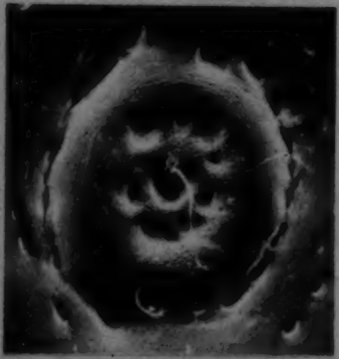
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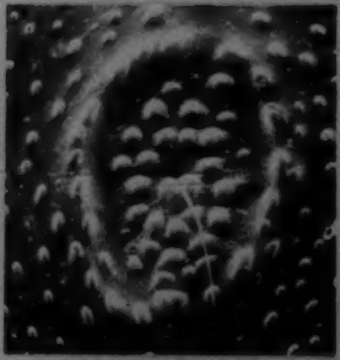
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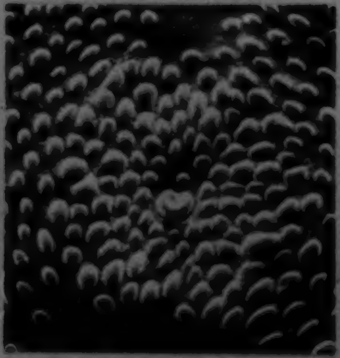
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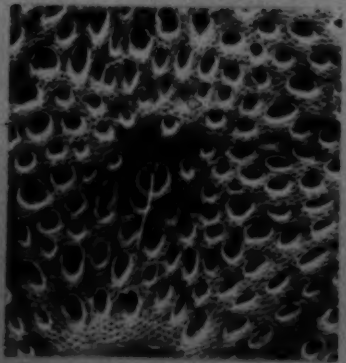
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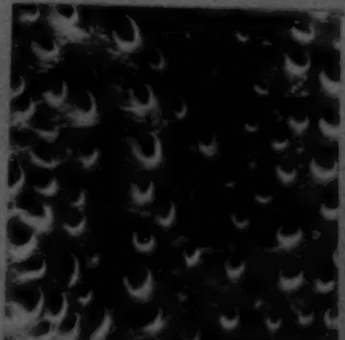
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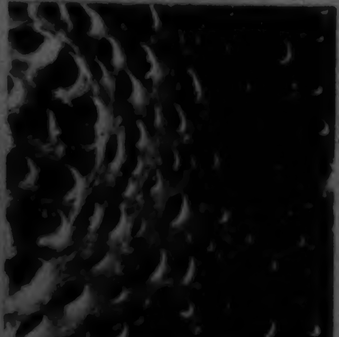
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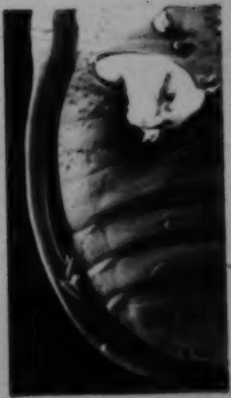
Fig. 139-148. Scanning electron micrographs of strucutres of adult Elaphrini. Fig. 139-142. Abdominal sterna. 139. *E. cicatricosus* LeConte, Maclean Bog, New York. 140. *E. californicus* Mannerheim, George Lake, Alberta. 141. *E. riparius* Linnaeus, Skane, Sweden. 142. *E. parviceps* Van Dyke, Thelon, Northwest Territories. Fig. 143-144. Type of microsculpture on abdominal sterna 4 and 5. 143. *E. riparius* Linnaeus, Skane, Sweden. 144. *E. parviceps* Van Dyke, Thelon, Northwest Territories. Fig. 145-146. Foreleg of *E. cicatricosus* LeConte. 145. Anterior aspect. 146. Posterior aspect. Fig. 147-148. Midleg of *E. cicatricosus* LeConte. 147. Anterior aspect. 148. Posterior aspect.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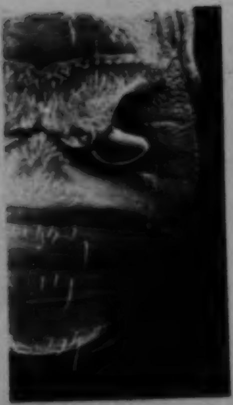
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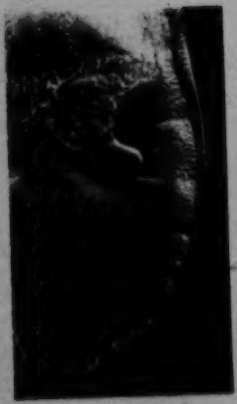
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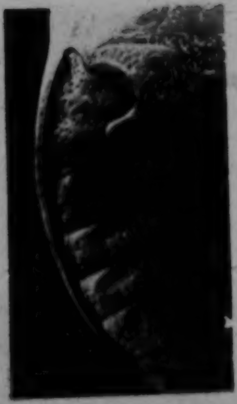
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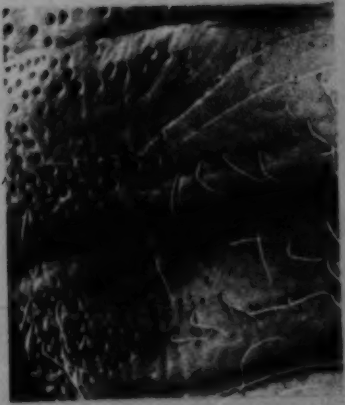
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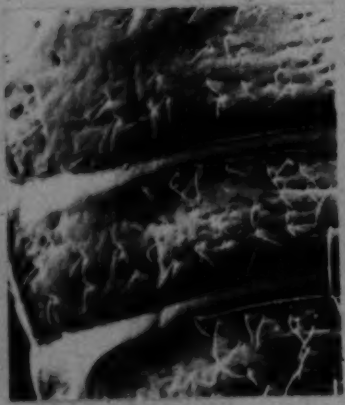
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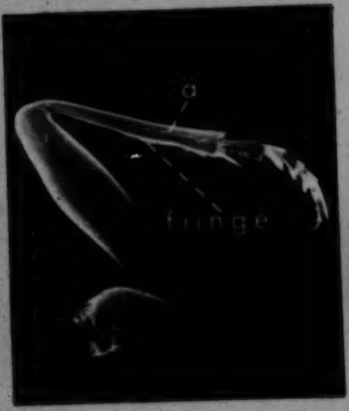

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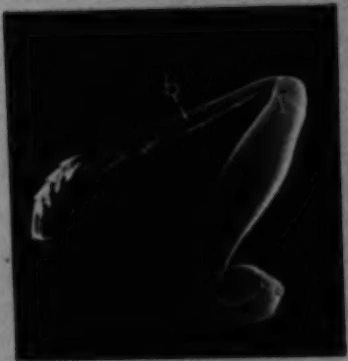

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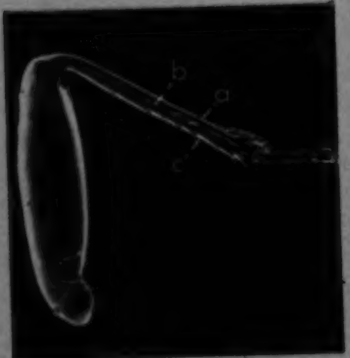
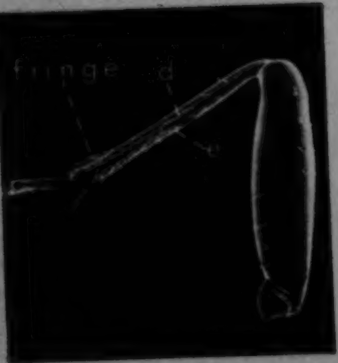
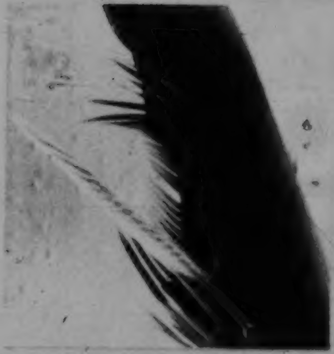


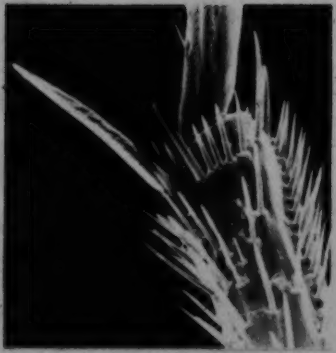
147

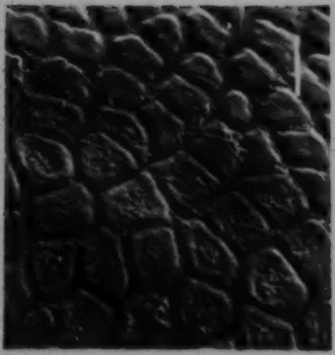


148

Fig. 149-156. Scanning electron micrographs of strucutres of Elaphrini. Fig. 149-150. Male adults of *E. Eicatricosus* LeConte. 149. Apex of foreleg, posterior aspect. 150. Apex of midleg, posterior aspect. Fig. 151-156. Types of microsculpture (white vertical line = 100 microns). 151. Isodiametric alveolae of microsculpture, upper third smooth alveolae, lower third punctate alveolae (brown areas)--based on third instar larva of *E. angusticollis angusticollis* Sahlberg. 152. Scale-like alveolae on side of head of third instar larva of *E. angusticollis angusticollis* Sahlberg. 153. Single-pointed scale-like alveolae on abdominal sterna of adult *E. riparius* Linnaeus. 154. Single, double and tripel-pointed microsculpture on tergum of third instar larva of *E. californicus* Mannerheim. 155. Raised multi-pointed microsculpture on abdominal sternum of third instar *E. californicus* Mannerheim. 156. Fine multi-pointed microsculpture on abdominal epipleuron of third instar larva of *E. angusticollis angusticollis* Sahlberg.


149


150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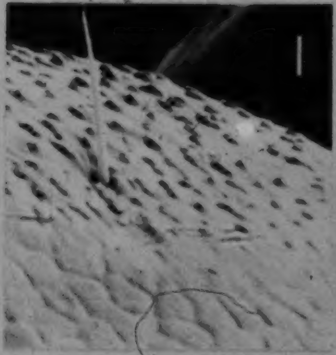
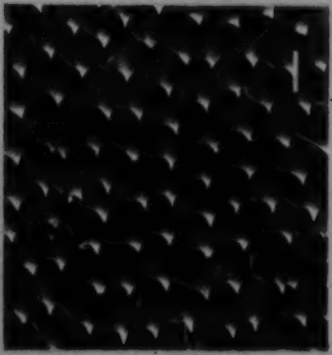
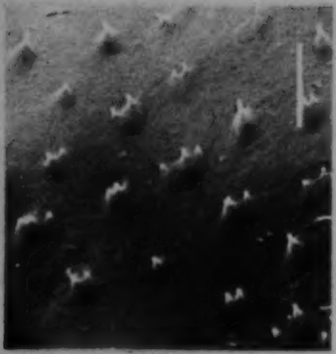
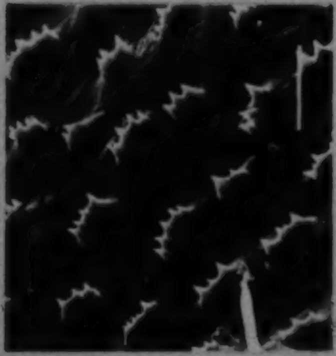

152


153


154


155

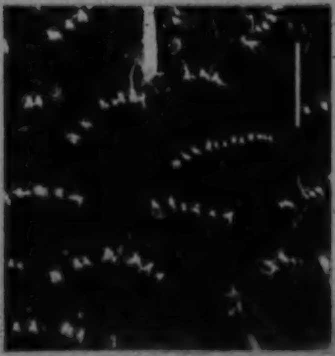
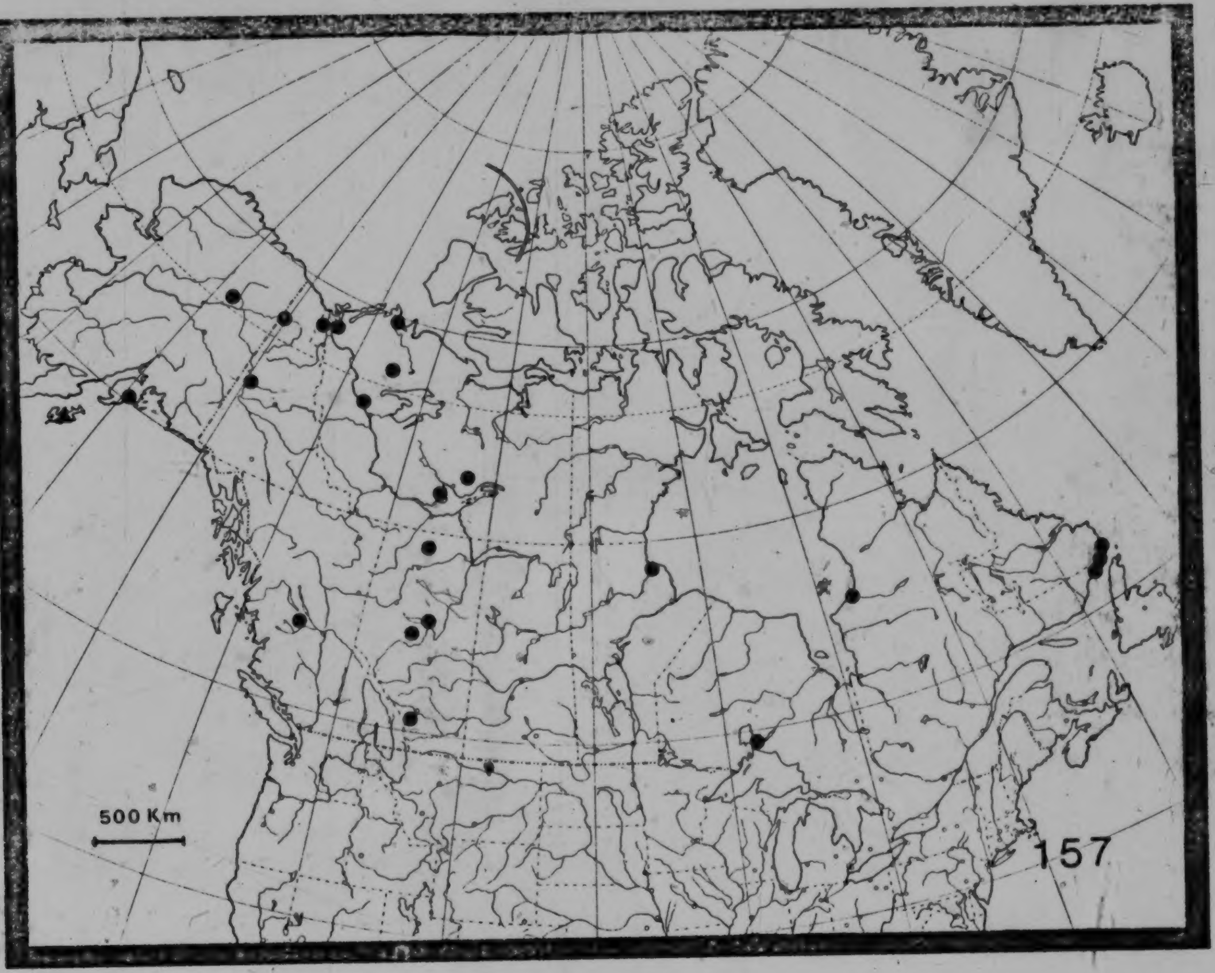

156

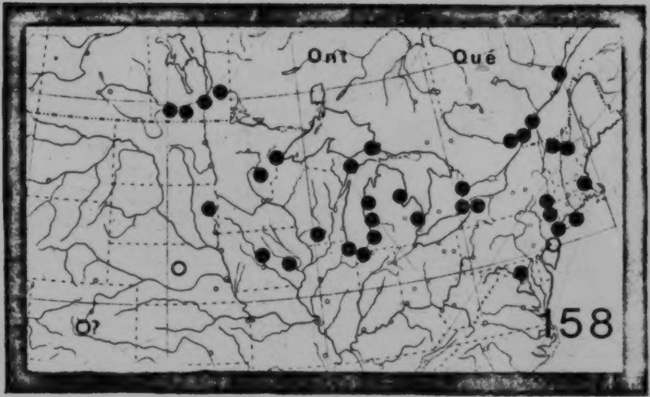
Fig. 157. Known distribution of *E. lapponicus lapponicus* Gyllenhal (circles) and *E. l. obliteratus* Mannerheim (triangles) in North America.

MARKS ON ORIGINAL

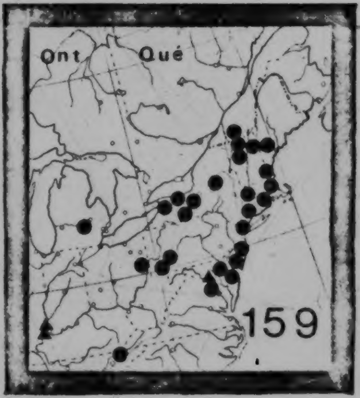


157

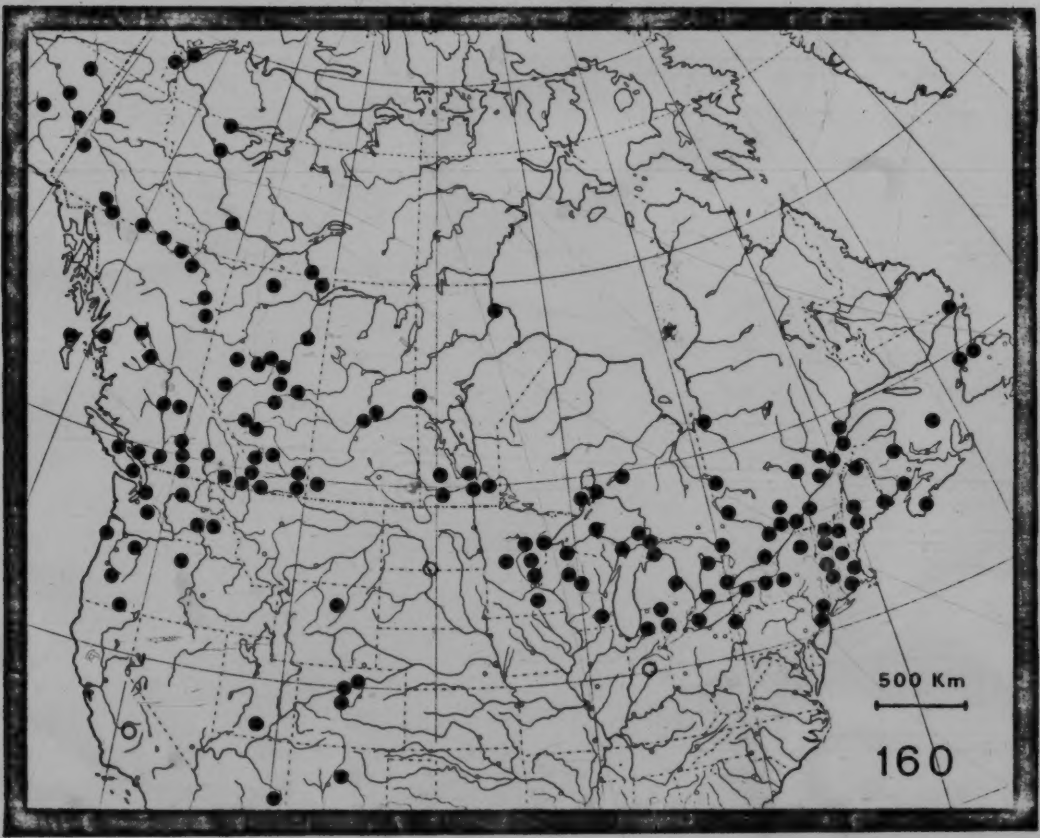
Fig. 158-160. Known distribution. 158. _E_. _fuliginosus_ Say. 159. _E_. _cicatricosus_ LeConte (circles), and _E_. _lindrothi_ new species (triangles). 160. _E_. _clairvillei_ Kirby.



158



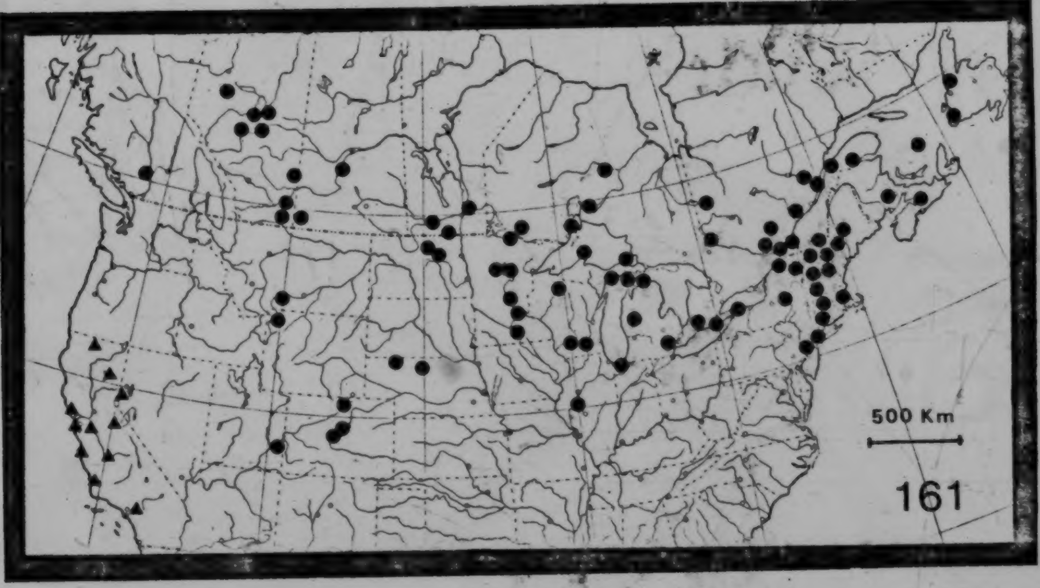
159



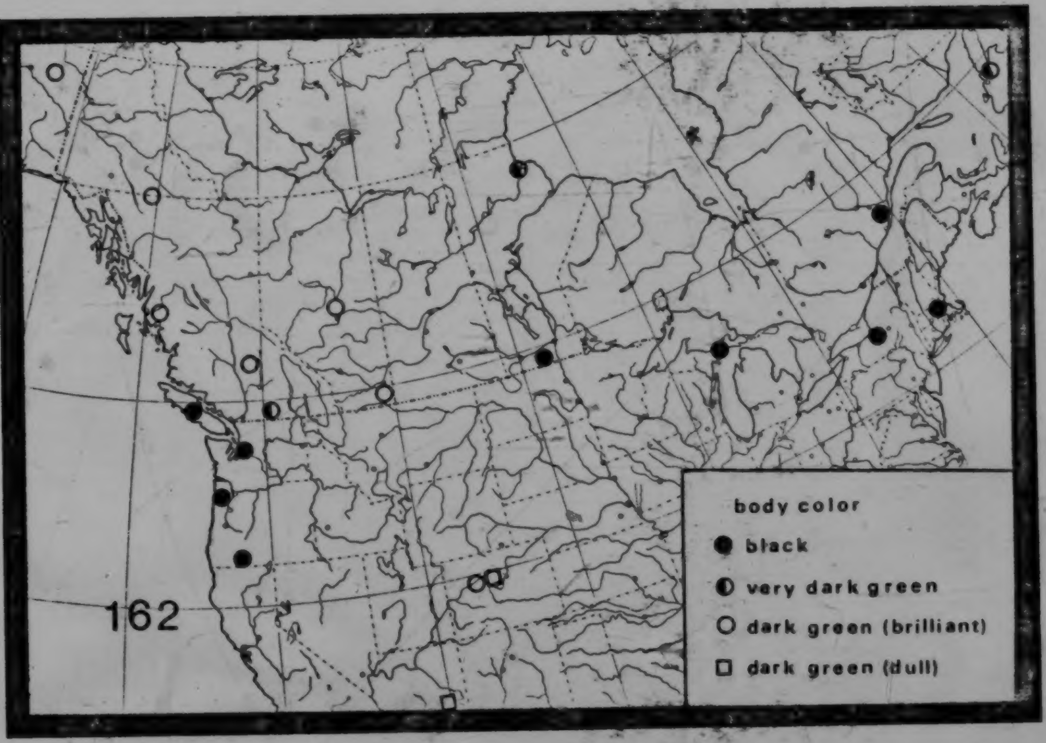
160

Fig. 161. Known distribution of *E. olivaceus* LeConte (circles) and *E. laevigatus* LeConte (triangles). Fig. 162. Variation in dorsal color of adults of *E. clairvillei* Kirby.

MARKS ON ORIGINAL

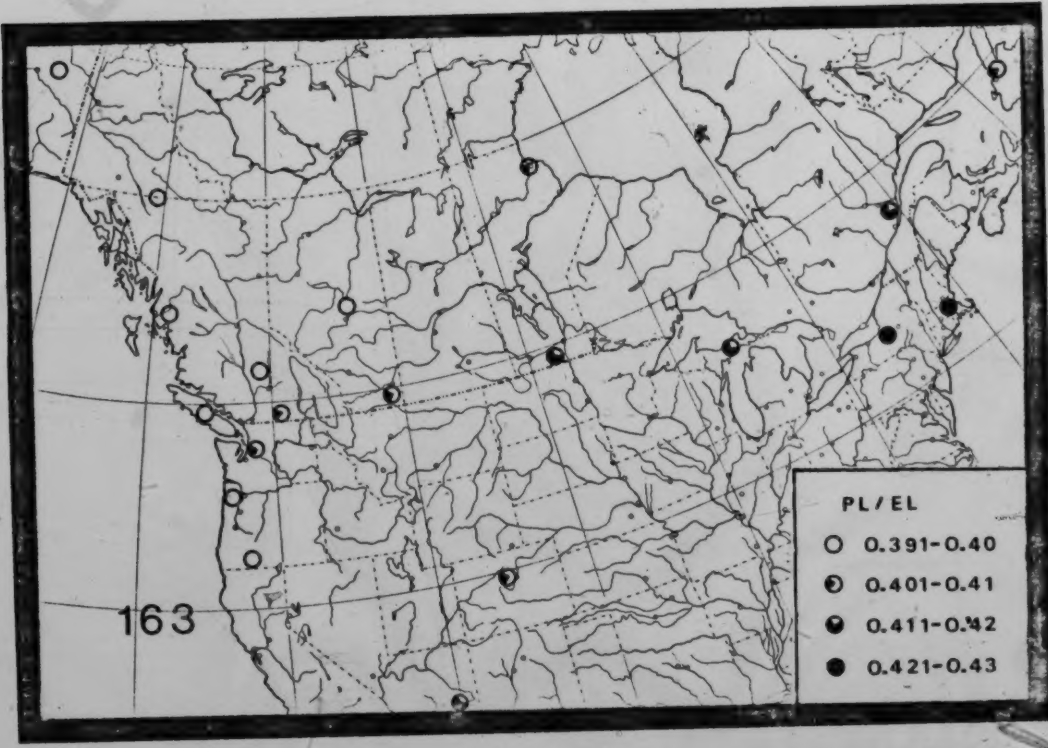

500 Km

161


body color
● black
◐ very dark green
○ dark green (brilliant)
☐ dark green (dull)

162

Fig. 163-164. Variation, based on adults of _E_. _clairvillei_ Kirby. 163. Ratio PL/EL. 164. Ratio PW/HW.


163
PL/EL
○ 0.391-0.40
◐ 0.401-0.41
● 0.411-0.42
● 0.421-0.43

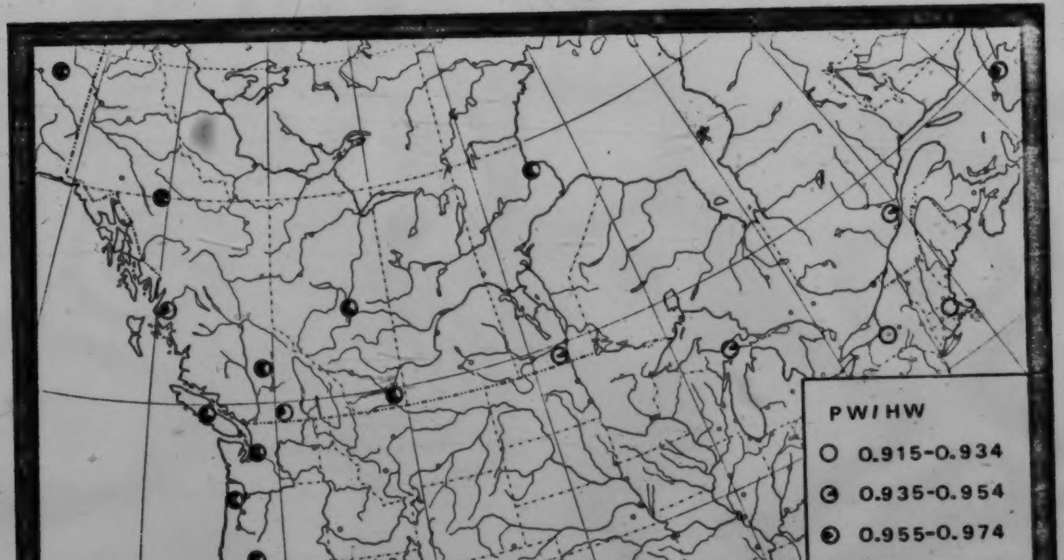
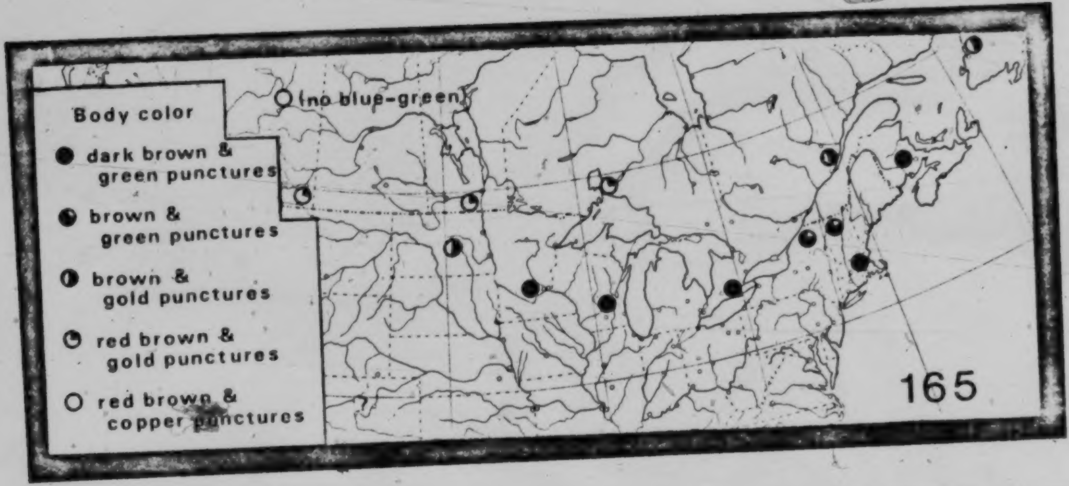
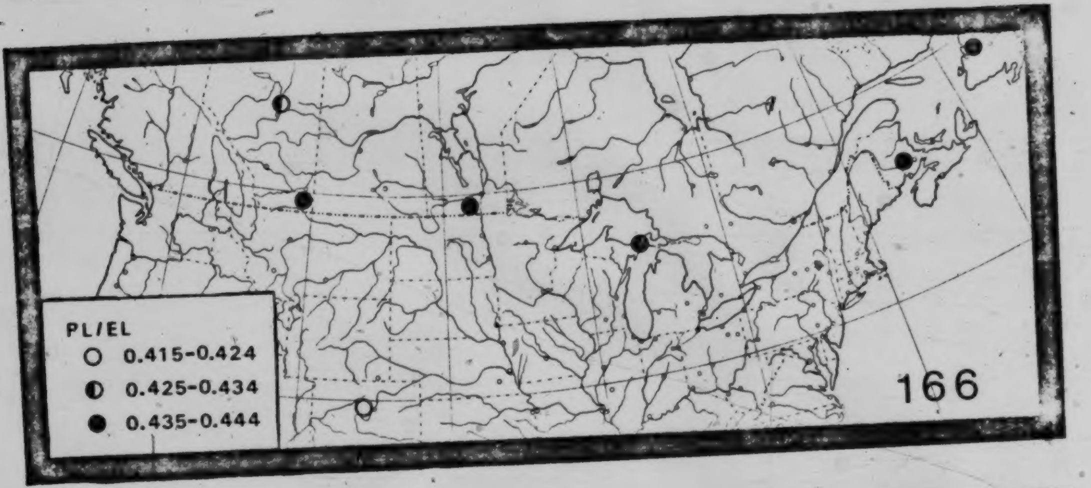

164
PW/HW
○ 0.915-0.934
◐ 0.935-0.954
◐ 0.955-0.974
◐ 0.975-0.994
● 0.995-1.014
● 1.015-1.034

Fig. 165-167. Variation, based on adults of *E. olivaceus* LeConte. 165. Variation of dark form and number of color forms in parentheies. 166. Ratio PL/EL. 167. Ratio PW/HW.


Body color
● dark brown & green punctures
◕ brown & green punctures
◐ brown & gold punctures
◔ red brown & gold punctures
○ red brown & copper punctures
(no blue-green)
165


PL/EL
○ 0.415-0.424
◐ 0.425-0.434
● 0.435-0.444
166

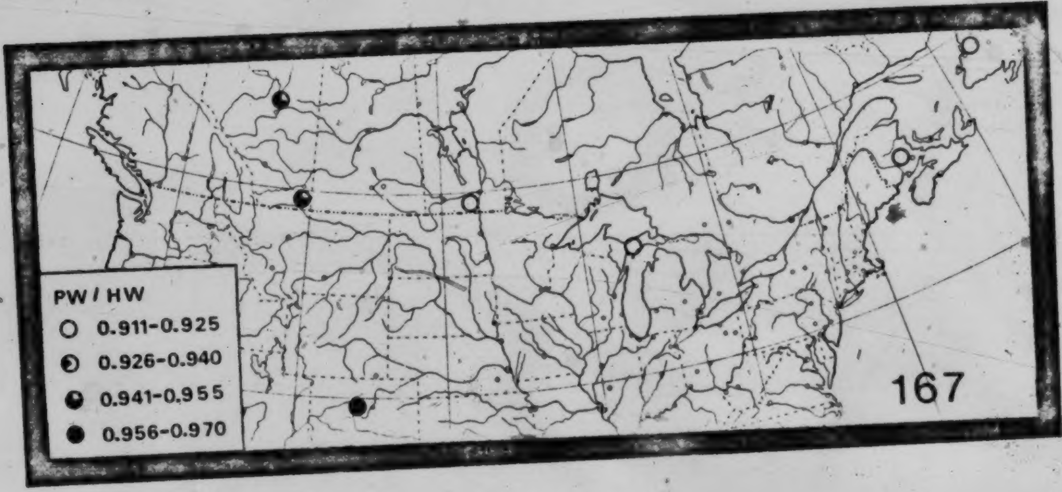

PW / HW
○ 0.911-0.925
◔ 0.926-0.940
◕ 0.941-0.955
● 0.956-0.970
167

Fig. 168. Phenetic relationships of genera and subgenera of Elaphrini based on a) adults, b) first instar larvae, and c) second instar larvae. See section 4.1.1 and Tables 30 and 31.

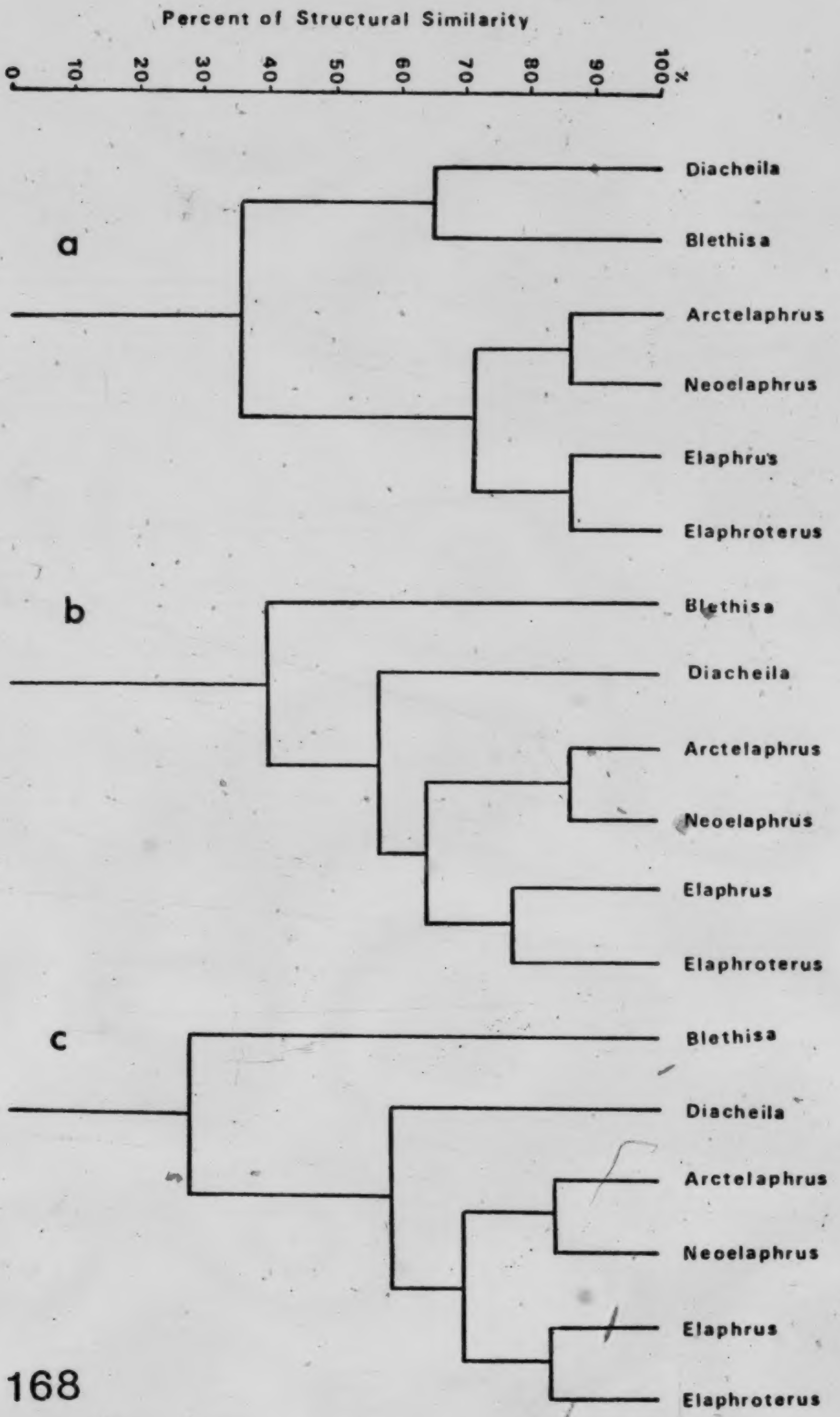
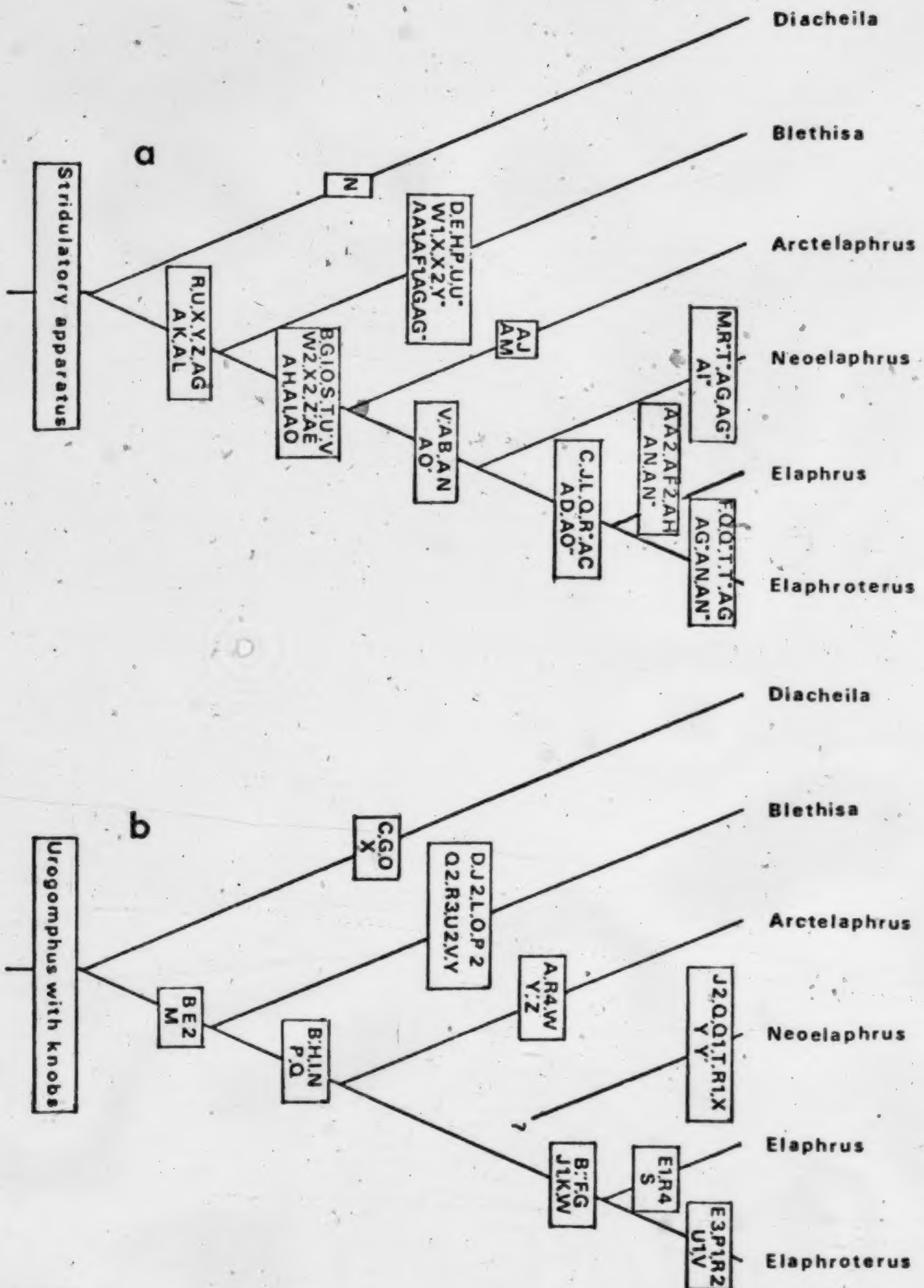

Percent of Structural Similarity
0
10
20
30
40
50
60
70
80
90
100
%
a
Diacheila
Blethisa
Arctelaphrus
Neoelaphrus
Elaphrus
Elaphroterus
b
Blethisa
Diacheila
Arctelaphrus
Neoelaphrus
Elaphrus
Elaphroterus
c
Blethisa
Diacheila
Arctelaphrus
Neoelaphrus
Elaphrus
Elaphroterus

Fig. 169. Reconstructed phylogeny of genera and subgenera of Elaphrini based on a) adults, and b) first, second, and third instar larvae. See section 4.1.2 and Tables 32 and 33.


a
Stridulatory apparatus
N
R,U,X,Y,Z,AG
A,K,AL
D,E,H,P,U,U'
W1,X,X2,Y'
AA1,AF1,AG,AG'
B,G,I,O,S,T,U',V
W2,X2,Z',AE
AH,AI,AO
AJ
AM
V',AB,AN
AO'
M,R',T',AG,AG'
AI'
C,J,L,Q,R',AC
AD,AO''
AA2,AF2,AH
AN,AN'
F,Q,Q',T,T',AG
AG',AN,AN'
Diacheila
Blethisa
Arctelaphrus
Neoelaphrus
Elaphrus
Elaphroterus
b
Urogomphus with knobs
C,G,O
X
D,J2,L,O,P2
Q2,R3,U2,V,Y
B,E2
M
B',H,I,N
P,Q
A,R4,W
Y,Z
J2,Q,Q1,T,R1,X
Y,Y'
?
B'',F,G
J1,K,W
E1,R4
S
E3,P1,R2
U1,V
Diacheila
Blethisa
Arctelaphrus
Neoelaphrus
Elaphrus
Elaphroterus

169

Fig. 170. Reconstructed phylogeny of sepcies of subgenus Neoelaphrus based on adults. See section 4.1.2 and Tables 34, 35, 36, and 37.

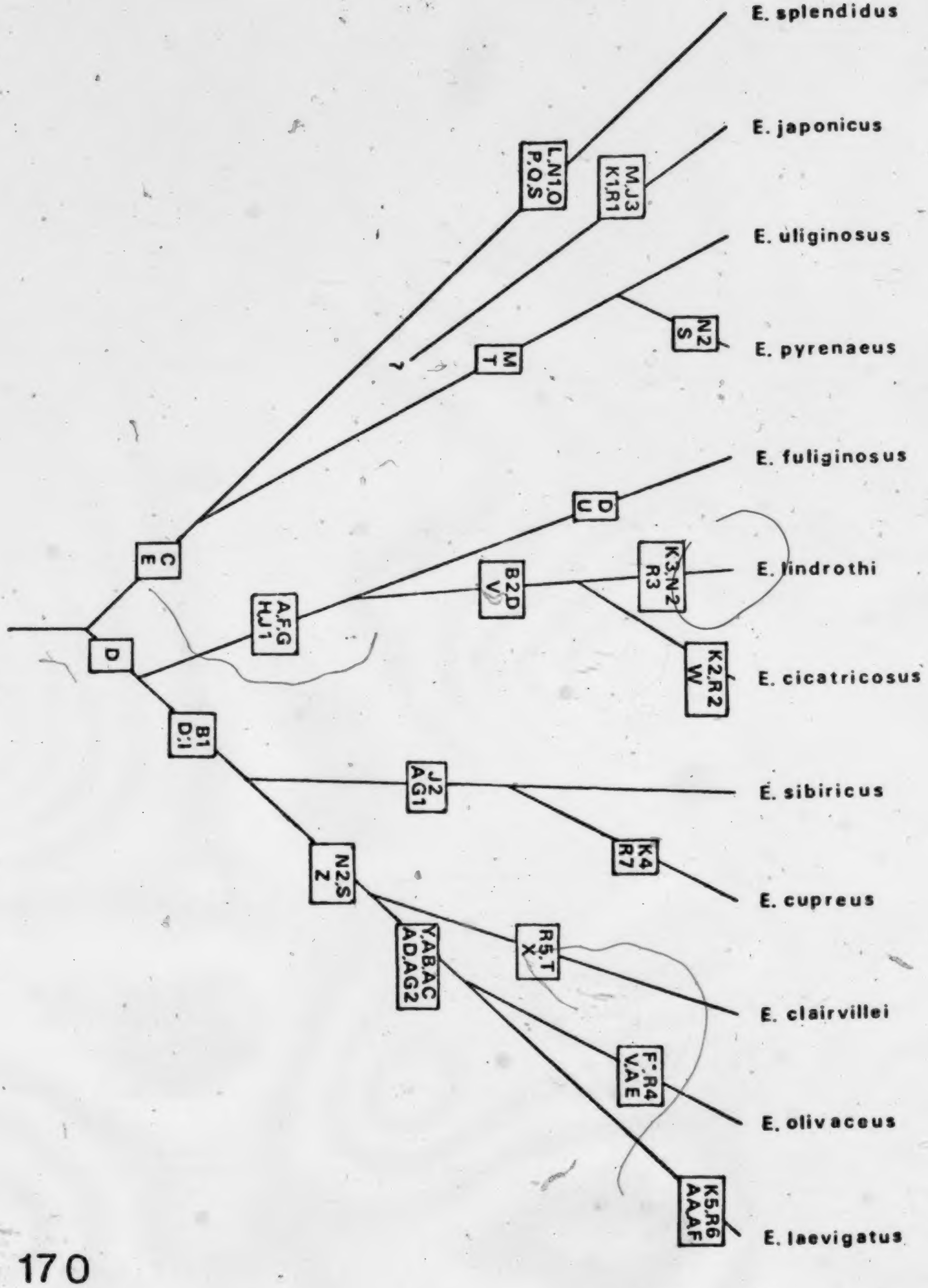

E. splendidus
E. japonicus
E. uliginosus
E. pyrenaeus
E. fuliginosus
E. lindrothi
E. cicatricosus
E. sibiricus
E. cupreus
E. clairvillei
E. olivaceus
E. laevigatus
L,N1,O P,O,S
M,J3 K1,R1
?
M T
N2 S
C E
D
A,F,G H,J1
D U
B2,D V
K3,N2 R3
K2,R2 W
B1 D:1
J2 AG1
K4 R7
N2,S Z
Y,AB,AC AD,AG2
R5,T X
F',R4 V,AE
K5,R6 AA,AF

Fig. 171. Correlation diagram for character states of habitat, and circadian activity among the species of Elaphrini.

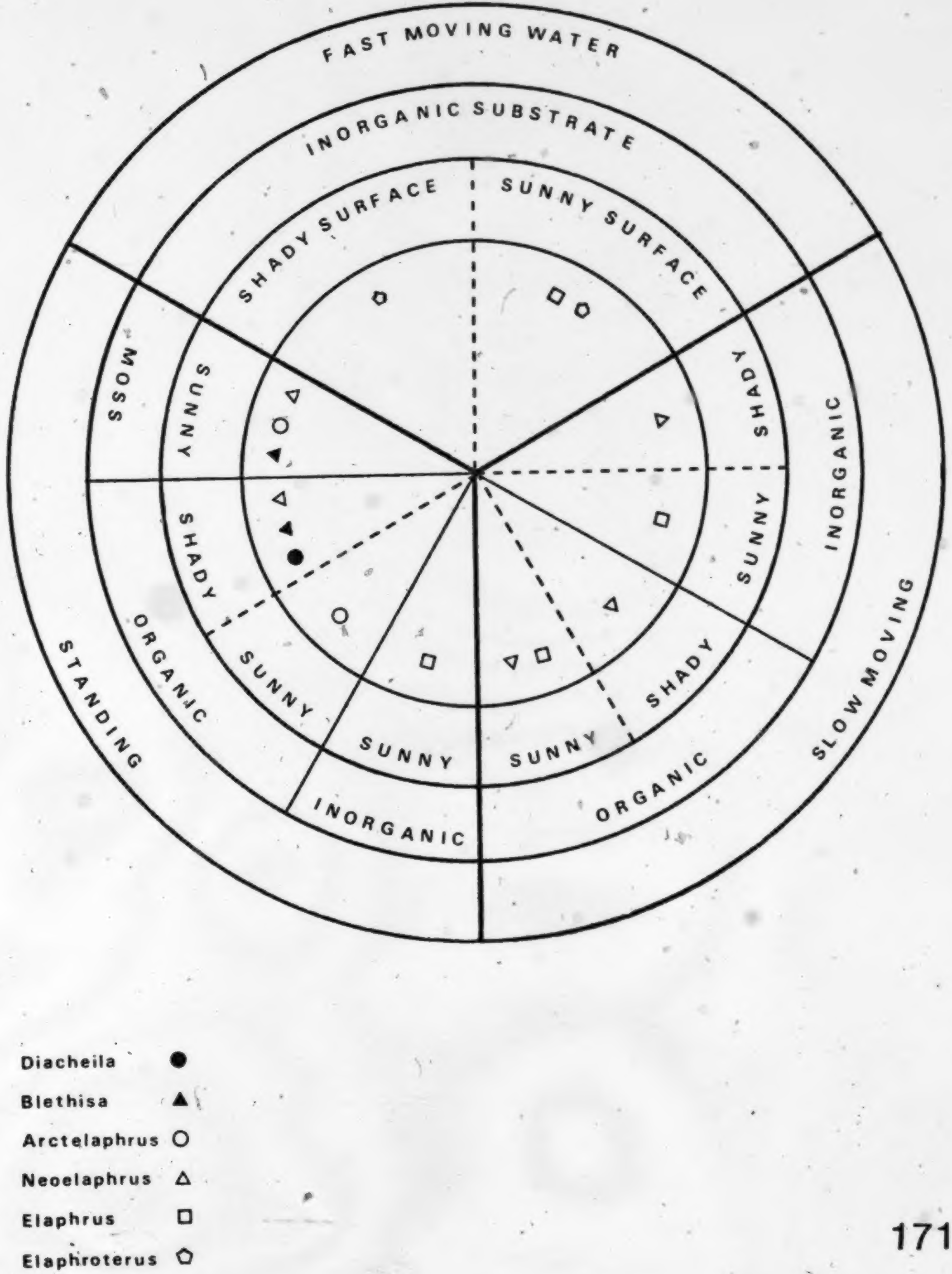
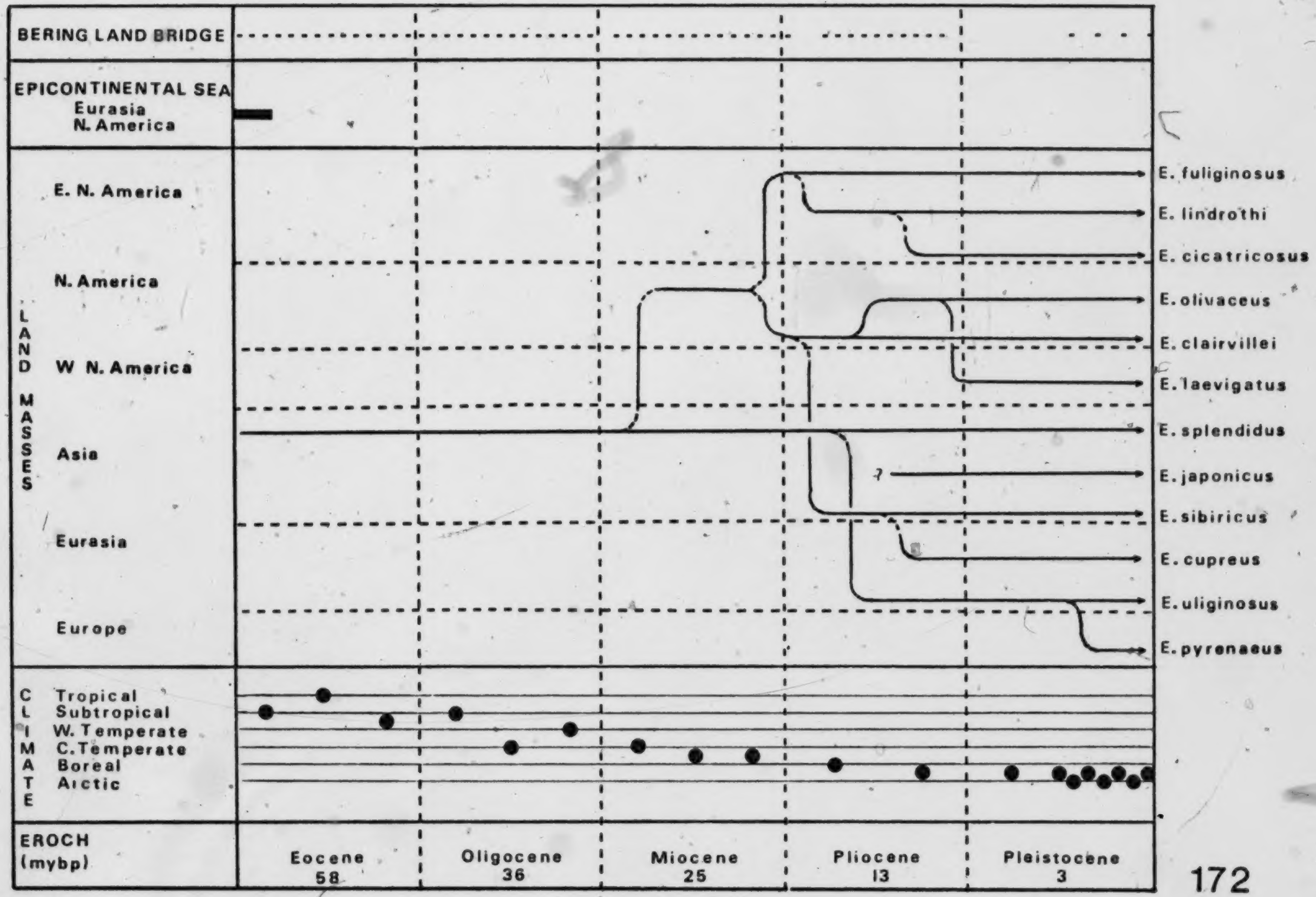

FAST MOVING WATER
INORGANIC SUBSTRATE
SHADY SURFACE
SUNNY SURFACE
MOSS
SUNNY
SHADY
SUNNY
SHADY
INORGANIC
SUNNY
SHADY
ORGANIC
SUNNY
SUNNY
SHADY
ORGANIC
STANDING
INORGANIC
SLOW MOVING
Diacheila ●
Blethisa ▲
Arctelaphrus ○
Neoelaphrus △
Elaphrus □
Elaphroterus ⬠

Fig. 172. Summary of probable zoogeographical events during the evolution of subgenus Neoelaphrus in Eurasia and North America. Their phyletic position is shown in Fig. 170. Climatic conditions are for Alaska for each period. The North American and Eurasian epicontinental seas are expressed as thick lines and the presence of land bridges as dotted lines in function of time.


BERING LAND BRIDGE
EPICONTINENTAL SEA
Eurasia
N. America
LAND MASSES
E. N. America
N. America
W N. America
Asia
Eurasia
Europe
CLIMATE
Tropical
Subtropical
W. Temperate
C. Temperate
Boreal
Arctic
EROCH (mybp)
Eocene 58
Oligocene 36
Miocene 25
Pliocene 13
Pleistocene 3
E. fuliginosus
E. lindrothi
E. cicatricosus
E. olivaceus
E. clairvillei
E. laevigatus
E. splendidus
?
E. japonicus
E. sibiricus
E. cupreus
E. uliginosus
E. pyrenaeus

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